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Full Name of Author — Nom complet de l'auteur

HELEN ANNE DUDYNSKY

Date of Birth — Date de naissance

13/08/54

Country of Birth — Lieu de naissance

CANADA

Permanent Address — Résidence fixe

300 Larch St - Sudbury ontario

Title of Thesis — Titre de la thèse

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Name of Supervisor — Nom du directeur de thèse

James M. Mayo / Keith E. Denford.

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THE UNIVERSITY OF ALBERTA

Photosynthesis and Water Relations in *Arctostaphylos uva-ursi* (L.) Spreng.

by

Helen A. Dudynsky

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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OF Master of Science

IN

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.....

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ABSTRACT

Two chromosome races of *Arctostaphylos uva ursi* were identified within the Kananaskis Valley, a recently deglaciated corridor abutting the eastern front ranges of the Rocky Mountains in Alberta. Occupying dissimilar habitats, the tetraploid and diploid populations were examined for physiologic differences which might coincide with the observed environmental separation of the races. It was found that the differences in photosynthetic capacities and water relations were maximized by mid to late summer. During this time the photosynthetic capability of the tetraploid was almost 300% higher than that of the diploid; chlorophyll b concentrations, implicated in enhancing net assimilation, were 20% higher, and cell walls were hydrostabile (rigid by two orders of magnitude) enabling the tetraploid to act as a water conserver. Downshifts in photosynthetic temperature optimum, Km values, transpiration rates, light compensation points as the summer progressed appeared to be larger for the tetraploid compared with the diploid, and effectively extended its growth season. It was concluded that the tetraploid 'maximizes' its open environment; that while it can occur in sheltered habitats, its physiological capabilities enable it to colonize much more severe and unstable environments and that the tetraploid is the ultimate pioneer.

PREFACE

ARCTOSTAPHYLOS, translated from the Greek, means bear's (*arctos*) grapes (*staphylos*). The specific epithet, *uva-ursi*, is from Latin and means *uva* (berry) and *ursi* (of the bear). The taxon has undergone periods of taxonomic revision and synonymy includes *A. officianalis* Willd., *Arbutus uva-ursi* Linn., and *Daphnidostaphylos fendleriana* Klot. Colloquially, it is known as arberry, mountain box, red berry, upland cranberry, meal berry, common bearberry, hog cranberry, whortleberry, larb, *Bousserole* (Fr.), *Barentraube* (Ger.), *kinnikinnick* and *sagakominagunj* (berry with spikes) by some North American Indians, *muskomina* by the Cree, *kasixie* by the Blackfoot (Murphy, 1959) and *sacacomis* by the voyageurs (Johnston, 1982).

Arctostaphylos uva-ursi belongs to the family Ericaceae. It is a trailing shrub with exfoliating, papery bark and evergreen, obovate to spatulate leaves and, unlike other ericoids such as *Ledum* or *Vaccinium*, it grows low to the ground. It forms dense mats on exposed rock, sand or glacial till but exhibits a 'looser' physiognomy when it occurs in association with grasses, herbs, other shrubs and evergreens (Fig. 1). Its habitat is limited to montane and occasionally subalpine regions and its worldwide distribution is circumboreal. In western North America, var. *coactilis* Fern. & Macbr. occurs as far south as northern California and east to northern Illinois (Fernald, 1950). The var. *adenotricha* Fern. & Macbr. (with glandular hairs) is found from the Côté Nord, Quebec to British Columbia and south to northern Minnesota and Montana. Wherever *Arctostaphylos uva-ursi* occurs it is as an important dominant or subdominant community member (La Roi *et al*. 1980, Birks, 1980, Ipatov *et al*. 1980, Bjorndalen, 1980 and Hansen, 1976).

As a medicinal herb *Arctostaphylos uva-ursi* has had a long standing service to man in both Europe and North America. The first recorded use of bearberry was in the 13th century where it was used as an astringent by the physicians of Meddfai. In 1763, Clusius incorporated it into the *London Pharmacopoeia* as a tonic tea and diuretic. Much later arbutin was found to be the effective agent (Frohne, 1970). Ample documents of native North American and European preparations and decoctions are well described in herbals by by Millspaugh (1982), Grieve (1931), Weiner (1972), Coon (1963) and Turner (1975).

The Coastal Indians of western North America called it *kinnikinick* or *sagakomi* and used it to extend tobacco as trade with white man increased. Actually, *sagakomi* is from the French (*sac-à-commis*) or clerk's bag and refers to the pouch in which the tobacco mixture was carried (Johnston, 1982). Pressed and dried, *Arctostaphylos* berries were quite useful. They were put into a dried fruit leather or mixed with other dried fruits into a kind of pemmican or used as beads in children's rattles. Blackfoot medicine men predicted a forthcoming harsh winter if the fruit set of bearberry was high (Johnston, 1982). In eastern Canada, the Chippewa (Ojibway) tribe brewed the leaves for tea to relieve headaches. The plant was also incorporated into their religion as a charm while an infusion of the berries, containing a high Vitamin C content, was made for use as a mouthwash for cankers and sore gums. Today, in commercial operations, tannins are extracted from the leaves and are used in Iceland, Sweden and the Soviet Union for tanning fine leathers.

Bearberry has been studied in many non-physiological aspects. For example the taxonomy of *Arctostaphylos uva-ursi* has been handled with versatility. Fernald and Macbride (1914) recognised three varieties according to vesture. Hulten (1948) added another. Calder and Taylor (1965), Wells (1968), Löve *et al.* (1971), and most recently Packer and Denford (1974) have examined taxonomic relationships introspectively with regard to ploidy. They discerned diploid, triploid and tetraploid populations, while Rosatti (1981) documented the *existenz* of a pentaploid from Long Island, New York.

Chemistry within the family Ericaceae has been well documented because of the number of compounds which can be easily detected by standard chemotaxonomic methods. Polyphenolic glycosides, arbutin, chlorogenic acid, flavonoid and quercitin constituents for example have been chromatographed and enumerated. Their appearance has been used by Denford (1973, 1981) in conjunction with morphological evidence to support traditional taxonomy and to compliment a theory of bearberry's phytogeographic distribution since the Pleistocene (Packer and Denford, 1974).

The name of bearberry is prominent in ecological studies. In North America, much of the extant work concerning the genus has been concerned with the ecology of Californian chaparral communities and the ericaceous manazanitas. These 'tree-shrubs' have a method of reproduction, fire resistance via the formation of burls and a mechanism

of shedding bark resulting in allelopathic interactions, which are similar to its northern counterpart *Arctostaphylos uva-ursi*. Leaf and bark leachates within the bearberry community, give it a pioneering advantage and their detrimental effect on seedling establishment of other species has been noted by Hannawalt (1971) and Richter (1981).

The pioneering capabilities of *Arctostaphylos uva-ursi* are particularily well known from studies of burn recolonization (Vogl and Schorr, 1972, Chou, 1973, Savage, 1974, Keeley, 1977 and 1978) and are linked to its nitrogen fixing ability (Allen *et al*. 1964, Stewart, 1976).

Seedling trials and artificial propagation for revegetation purposes have been conducted as early as 1937 (Griesbach, 1937) and there has been a strong Russian interest in this area (Pyasyatskene, 1975).

Physiologic oriented work on bearberry is limited and descriptive. But Shaver's (1978) work, because of its individual nature and also because of its pertinence to net assimilation (NA) results, will be interperted physiologically. He described a continental transect from the seacoast inland, measuring leaf angle and orientation in a number of *Arctostaphlos* species. Low light, low temperature species held their leaves more horizontally, while high light, high temperature species held their leaves tightly together in a more vertical position as was observed in the populations studied here. This posture may have some significance to photosynthetic capability, specifically, in determining the facility with which stomatal gas exchange occurs.

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Glossary of Scientific Abbreviations used throughout the Text

CEC: controlled environment chamber

Chl a: chlorophyll a

Chl b: chlorophyll b

DMSO: dimethyl sulphoxide

DR: dark respiration

F: field material

GH: greenhouse grown

GHR: greenhouse roof grown

GRZ: Grizzly Creek

HO: Hill Open

HU: Hill Under

IRGA: infrared gas analyzer

LCP: light compensation point

NA: net assimilation

ND: no data

P-V: pressure-volume

Ps: photosynthesis

PSII: photosystem II

Rbnside: Ribbon Creek Side

Rbntop: Ribbon Creek Top

SQ: Squirrel

SI: Stomatal Index (See Appendix II)

VAT: value average turgor

veg.= vegetative

VPG: vapour pressure gradient

VPD: vapour pressure deficit

XPP: xylem pressure potential

π_0: osmotic potential

πp: osmotic potential at incipient plasmolysis

I. INTRODUCTION

The concern of this work is to reveal the importance of ploidy in *Arctostaphylos uva-ursi* as it relates to its physiology. Historically, polyploidy has been viewed broadly from an ecological and taxonomic perspective. It is interpreted as confering on a species an adaptive superiority to *severe* environments. Hagerup (1931) was the first to suggest this. Love and Love (1957) followed, surmising that the incidence of polyploidy would increase with increasing latitude. The inherent problematic simplicity of this interpretation became evident as Johnson and Packer (1968) found that the occurrence of polyploidy at Ogotoruk Creek in northwestern Alaska was not as great as in areas of similar latitude in Europe. Dobzhansky *et al.* (1977) found that polyploids can occur in habitats which are more mesic than those of the progenitor diploids.

It seems that this ancestral approach to the question of evolutionary success of increased ploidy (it appears in 30% of all angiosperm genera, Stebbins, 1938) has too broad a basis and has lead to a vastly oversimplified interpretation of distribution patterns and the success of polyploids. On the other hand, the contemporary impetus of research, as evidenced by the first international conference on polyploids (Lewis, 1979), has become very reductionist. It narrowly focuses, for example, on quantifying subcellular components – DNA, RNA, or isozymes (Tal, 1979) in easily scrutinizable agronomic crops with varying ploidy such as *Lycopersicon esculentum* (tomato) or *Avena sativa* (oats), *Nicotiana tabacum* (tobacco), or weedy plants such as *Datura* (jimsonweed) and *Vicia* (vetch). This single factor approach omits the interim level of investigation dealing with the modes or processes that link the subcellular, whole plant and community levels together. A physiological understanding seems lacking in considering the role of polyploidy in natural evolution. Describing them, as is the aim of this study, could substantiate the distribution patterns, provide a *raison d'être* of polyploidy and test the theory that increased ploidy means increased physiological adaptation. Thus, it might be said that few bridges have been built between the traditional realms of taxonomy, chemotaxonomy and physiology, *i.e.* there is excessive segregation and that, as such, there is a need for a balanced hybridity which would lead to a breed similar to Mooney and Billings' (1961) physiological ecology, an ecophysio-taxonomy of renewed vigour in scientific approach and scrutiny.

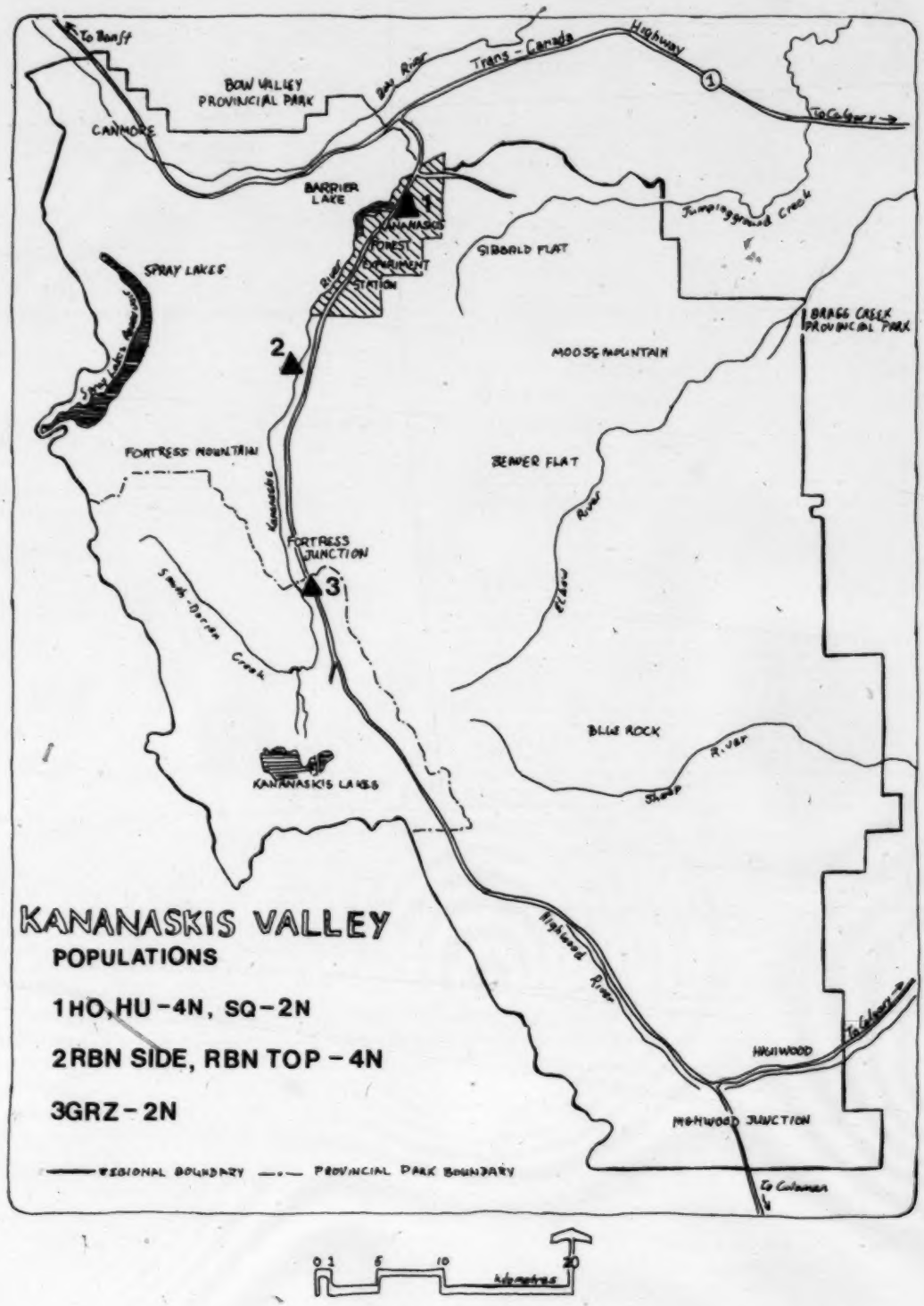
A trend for such a salamagundi of investigative force appears, albeit slowly, to be emerging. In so doing, the investigators are actually "Zoranthustrians searching for the higher plant" (J. Mayo, pers. comm.). Tregunna et al., (1970), for example, described a methodology which involves the use of chromatography, isotope discrimination, leaf anatomy and CO_2 compensation points to classify angiosperms into C_3 and C_4 categories in an amalgamation of physiology and taxonomy. Albuzio *et al.* (1978) have described the water relations of several polyploid species. Mauer et al. (1978) compared the ecophysiology of chromosome races of *Viola adunca* with respect to photosynthesis and water relations in diploid and tetraploid populations. They found no significant differences between the ploidy levels. However, Davis (1980) examined the hardiness and productivity of the same species and did find differences. Without hardening, the tetraploid was more able to withstand a cold period. The diploids had only a 53% survivorship rate, while the tetraploids had a 100% rate, at a stress temperature of −6°C. Both seed set and root to shoot ratio were higher in the tetraploid indicating the advantage of enhanced ploidy level *per se*. The diploid showed a particular tenacity within its area of colonization, and the tetraploid showed the ability to colonize new habitats in the absence of the diploid relative.

Chromosome complement can be increased by a doubling of the genome in which case an autopolyploid is produced (most typical), hybridization in which case an allopolyploid is produced, or through cryptic polyploidy in which the DNA/chromosome ratio increases. Populations of *Arctostaphylos uva-ursi* contain both autopolyploids and allopolyploids (Packer and Denford, 1974) which have probably arisen within suspected refugia in the Rocky Mountains (Denford, 1973).

This study was done during two natural growing seasons in the summers of 1979 and 1980. It compared sympatric diploid and tetraploid races which were found to occupy distinct habitats – sheltered and exposed. Parameters in photosynthesis and water relations at the cellular and whole plant levels were examined. The data gathered were then compared and related to ploidy. The sociobiological role of bearberry in the *Pinus contorta/Shepherdia canadensis/ Arctostaphylos uva-ursi* community was considered and finally, in a synthesis, the data was extrapolated to infer the colonizing potential of the diploid and tetraploid populations in areas deglaciated since the Pleistocene.

II. METHODS AND MATERIALS

Figure 1. The location of Arctostaphylos uva-ursi populations studied within the Kananaskis Valley. The populations Squirrel, Hill Open and Hill Under are located in the proximity of Barrier Lake and the Kananaskis Environmental Centre (1) Ribbon Top and Ribbon Side (2) at the Mt. Allen trailhead and Grizzly Creek (3) is 16 miles south of the station along the Trunk Road to Highwood Pass.


To Banff
BOW VALLEY PROVINCIAL PARK
Bow River
Trans - Canada Highway
1
To Calgary
CANMORE
BARRIER LAKE
1
KANANASKIS FOREST EXPERIMENT STATION
Jumpingground Creek
SIBBALD FLAT
SPRAY LAKES
River
BRAGG CREEK PROVINCIAL PARK
2
MOOSE MOUNTAIN
FORTRESS MOUNTAIN
BEAVER FLAT
Kananaskis
River
FORTRESS JUNCTION
3
Elbow
South-Darien Creek
BLUE ROCK
River
Sheep
KANANASKIS LAKES
KANANASKIS VALLEY
POPULATIONS
1HO, HU-4N, SQ-2N
2RBN SIDE, RBN TOP-4N
3GRZ-2N
Highwood River
To Calgary
HIGHWOOD
HIGHWOOD JUNCTION
REGIONAL BOUNDARY
PROVINCIAL PARK BOUNDARY
To Coleman
0 1 5 10 20
Kilometres

II. METHODS AND MATERIALS

The two major criteria in locating an appropriate study area were: 1) a geographic area which was once glaciated, and 2) a vegetation community in which *Arctostaphylos uva-ursi* was either a dominant or codominant understory shrub in sufficient abundance to withstand intensive sampling. With this in mind, directed by both a University of Calgary herbarium specimen which indicated a tetraploid population at Ribbon Creek ,Kananaskis Valley, and a reference in Packer and Denford (1974)to a refugial population of diploid *Arctostaphylos uva-ursi* at Grizzly Creek, Kananaskis Valley, a visit was made to these two creeks. The Kananaskis Valley is 45 miles west-southwest of Calgary and is a postglacial corridor aligned in a north-south direction with the Eastern Front Ranges of the Rocky Mountains. The University of Calgary's Environmental Research Centre at the north end of Barrier Lake was soon realized as the main stage, providing literally a centre to radiate out from when field work was required. Three study areas were chosen within proximity of the Centre (Fig. 1). Ribbon Creek was 15.8 km south of the Centre. The Grizzly Creek site was 23 km further south from Ribbon Creek and the third area was selected immediately near and within walking distance of the Centre.

The term *population* is used here in a liberal sense to mean a landform-cover entity of a particular ploidy level. The landform is *e.g.* a fluvial fan, morainal deposit or avalanched terrain, with a large *Arctostaphylos uva-ursi* diploid or tetraploid mat. The term *site* will be used interchangably with *population*. For example, *Squirrel* indicates the squirrel midden site and represents a diploid population.

At the end of two field seasons, a total of six populations/ sites, three of each diploid and tetraploid levels, had been determined morphologically according to Packer and Denford (1974) and later verified by a chromosome count. The designation of the populations are found in Table 1. Nomenclature there bears no direct importance to the present study so that the names of the taxa are eventually dropped and the results are discussed throughout the text in the generalities of a diploid or tetraploid identity. However, the most commonly used live diploid material was from the *Squirrel* site because it survived the transplant and greenhouse propagation. Similarly, the representative tetraploid population was from the *Ribbon Creek* study area.

TABLE 1. A SYNOPSIS OF SITES, PLOIDY, & TAXONOMIC IDENTITIES FOR 6 POPULATIONS OF ARCTOSTAPHYLOS UVA-URSI STUDIED

Ploidy	Chromosome #	Site name and abbreviation	Taxonomic Identity of *Arctostaphylos uva-ursi*
DIPLOID	2N = 26	Grizzly Creek (GRZ)	ssp. *adenotricha*
		Squirrel (SQ)	ssp. *adenotricha*
		Ribbontop (Rbntop)	ssp. *adenotricha*
TETRAPLOID	2N = 52	Ribbonside (Rbnside)	S+1+ unnamed
		Hill Open (HO)	ssp. *uva-ursi*, var. *coactilis*
		Hill under (HU)	ssp. *uva-ursi* var. *uva-ursi*

Ploidies as determined by root tip and bud squash preparations (via a Cooperrider-Morrison (1967) & Tijo & Levan (1950) hybrid method) fall neatly into two categories, diploid and tetraploid. The entities were identified and a subspecific epithet attached to each according to the taxonomic treatment of Packer & Denford (1974). To ease the reading of the text the populations will subsequently be simply referred to as the diploid (2N) or tetraploid (4N) populations. For the experiments HO & HU material was rarely used. GRZ (2N), SQ (2N) and RBNside (4N) were the populations compared most frequently.

The characteristics which visually differentiate the ploidies and were the basis on which populations were originally chosen and identified before chromosomal determination are shown in Figs. 2A and 2B.

A. Site (Population) Descriptions

An abbreviation of the site name accompanies each description and a community composition is given for each population in Appendix I. In general the tetraploid occurs in a much more rigourous environment, experiencing sharper gradients in diurnal temperatures especially during the spring and autumn, wind exposure which enhances desiccation in summer and winter, abrasion and mechanical damage, and in light intensity. The diploid occurs in a more mesic environment , sheltered beneath a canopy of *Pinus contorta*. The plants are semishaded and experience fewer fluctuations of temperature, humidity, factors which might affect CO_2 availability, wind exposure, winter desiccation, abrasion, air movement, water availability and incoming solar radiation. The soils also are more developed resulting in water retention. Diploid bearberry is a codominant in the herb layer rather than the dominant (as the tetraploid is) in its community. It therefore experiences more competition with other shrubs, grasses, etc. for nutrients. It is also not the only nitrogen fixer in the community since *Shepherdia canadensis* has nitrogen fixing rhizobial activity associated with its roots.

Squirrel (SQ) (2N)

This study site was named after a multi-generation squirrel midden which sat roughly in midplot. It was approximately one-quarter mile along the trail which follows the Centre's water supply. Physiographically, it is on a fluvial fan with a 5% slope and a northwest aspect. Of all the sites, the environment of the diploid *Squirrel* population is the most sheltered and buffered from extremes of sunlight intensity and changes of humidity, temperature and wind. Sunlight filters through a closed canopy of *Pinus contorta* and *Populus tremuloides* which provides a constant partial shade at ground level. A stream abuts the study site a meter away, providing an aesthetic gurgle to take measurements by. The soil is well drained and has a thin Ae horizon. (The soul of bear-berry is here.) The community of this site has a higher diversity of species than occurs at

Fig. 2A and 2B. The typified physiognomy of diploid and tetraploid Arctostaphylos uva-ursi.

Fig 2A. A branch of Arctostaphylos uva-ursi sensu lato of diploid (2N) type. The leaves are obovately shaped and occasionally have apices which are retuse. They have a thin cuticle, are visibly a darker green than the tetraploid, are flexible and bend easily without breaking. Below it is a 'loose' mat physiognomy of the diploid as it grows beneath a Pinus contorta canopy.

Fig. 2B. A typical branch of tetraploid (4N) A. uva-ursi sensu lato has spatulate leaves. Unlike the horizontally displayed 2N leaves those of the 4N are tightly appressed to the stem. The physiognomy of the mat is a tight and dense formation and the mats occur in open exposed environments. The leaves are thickly cuticled, are olive green in colour and they snap in two when they are bent.

the other sites. Snow depths were considered as part of the assessment of the environment which the population experiences. Spring snow depths observed in April 1980 were 15-25 cm. The population here presumably experiences little or no winter abrasion by wind-driven snow.

Grizzly Creek (GRZ) (2N)

Arctostaphylos uva-ursi var. *adenotricha*, a diploid, occurs here on a southwest facing, terraced, 35% avalanche slope in an open forest of immature *Pinus contorta*. The forest physiognomy of clumped trees appears to provide a semi-sheltered environment which moderates the fluctuations in air temperature, air circulation, and humidity. *Arctostaphylos uva-ursi* occurs primarily in the openings between the pines and spruces.

Hill Open (HO) and Hill Under (HU) (4N)

These populations occur on a hill made of glacial till on the east side of the road which descends to the Provincial Parks compound and the Kananaskis Centre turnoff. The hill itself is crowned with an old fire tower lookout and is part of the Alberta Parks interpretive loop which starts from the Information Centre. The aspect is northwest and the slope is 28%. The two populations are taxonomically different. HO is *Arctostaphylos uva-ursi* var. *coactilis* and HU is *Arctostaphylos uva-ursi* var. *uva-ursi*. Both are tetraploid and are contiguous with each other through an ecotone. HU refers to a closed canopy of *Pinus contorta* and is sheltered compared to the exposed, open slope and shrub dominated community of HO.

In HO, the tetraploid *Arctostaphylos uva-ursi* occupies a greater portion of the ground cover than in HU. Snow depth is 10-20 cm in the winter.

Ribbon Creek (RBN Top and RBN Side) (4N)

The *Ribbon Creek* sites are situated to the west of the limestone quarry at the head of the Ribbon Creek Trail (the Mt. Allan trailhead at the parking lot). The site is a glacial till knoll overlooking Ribbon Creek itself. *Ribbon Creek Top* is an exposed site which supports two sympatric populations of *Arctostaphylos uva-ursi* of differing chromosome number. A small, local population of diploid *adenotricha* and also a tetraploid of unnamed

status (S+L+vesture, Table 1) occur at the top of the knoll. It is impossible, without destroying the population, to determine if the diploid is a single proliferating plant or if the tetraploid is of the same plant. It was assumed that the populations consisted of several individual plants.

RBN Top and RBN Side are part of a sympatric population covering approximately 55-75% of the slope. The angle of the slope varies from 55-75% and the aspect is from southwest to southeast. Most exposed of all the sites, *Ribbon Creek* also has the least snow. Winter snow depth is only about 20 cm because of the exposure. The site experiences high insolation, a full range throughout the day, and hence, a high fluctuation in diurnal temperature. The site has a particularly short day in autumn because of the surrounding mountains. The leaves of these populations were thickly cuticled, which is probably an adaptation to the higher water stress and inreased UV light intensity in an exposed environment.

B. Collection and Propagation of the Populations

Plants were taken from the field with a large portion of native soil intact around the stout rhizome. The three major techniques used included: rooting of cuttings in perlite, solution cultures and growing mats of the intact field material in greenhouse seed propagation trays. The technique used depended upon the type of experiment in which the plant material was to be used.

Plants which were used for water relations and photosynthesis experiments were repotted into flats in the lab in the native soil and a 1:1:1 mixture of peatmoss, sand and potting soil (greenhouse prepared). Because of the trailing habit of the plant, the flats proved ideal. Some were segregated into various greenhouses as space allowed, others were planted outdoors in beds alongside the greenhouses. To prevent oversaturation and waterlogging of the soils, they were watered approximately every three days and received a fertilizer treatment every six months.

To provide material for chromosome root tip squashes, rooting trials were conducted with the help of Dick Hillson, Research Associate in Forest Science. Multiply branched twigs were selected from field material, snipped off and the cut ends were treated with 2500 or 10,000 ppm of IBA and Seradix 3. These were placed in perlite for

1-1.5 months in a mist chamber until the root systems were fully developed usually to a length of 2.5 cm. They were then transferred to pots in the greenhouse. Occasionally for the chromosome studies, cut branches (usually winter field tissue) were solution cultured (Bot. 324-325 Plant Physiol. Lab. Man. 1980-1981). The twigs were gently aerated via a pipette hooked to an air supply. This method proved very successful and provided an additional source of root tips.

C. Chromosome Determinations

To induce maximum mitotic activity in the root tips, plants grown in flats were deprived of water for one day and then amply watered on the day prior to root tip harvest. The method of mist chamber propagation and the water cultures dispensed with the pretreatment just described and thus facilitated a continuous harvest. Both methods were used to provide an adequate supply of chromosomal material.

Root tips were dipped into precooled vials of oxyquinoline and processed according to the method of Tjio and Levan (1950) as detailed by Mauer (1977) and Davis (1980). After three hours at 12°C, squash preparations were made and stained by the method of Cooperrider and Morrison (1967). In this method, a lacto-acetic orcein stain was used in lieu of an acetic orcein stain. Penetration and staining quality of the chromatids was much improved and the preparation time from squash to observation was shortened. Precursory heating in a watchglass was eliminated and the condition of *refried genes* was avoided. A drop of Hoyer's solution (Flint, 1975) was added to the stained specimen and acted as a cellular clearing agent, improving the clarity of chromatid observation. Counts were performed using a Zeiss HA compound binocular microscope with green filters which enhanced the contrast between the stained chromatids and other cellular contents.

D. Water Relations

Vapour Pressure Deficit (VPD) measurements

Greenhouse material, acclimatized for approximately one year, was used to determine the transpirational (TSP) response of *Arctostaphylos uva-ursi* over a range of vapour pressure deficits (VPD). Twigs were cut under water to prevent air embolisms in the xylem issue and then individually sealed in preweighed 25 ml beakers with parafilm (Mayo and Ehret, 1980). They were placed into mini-controlled environment chamber desiccators with adjusted relative humidities of 8%, 50% and 80% (Winston and Bates, 1960). Transpiration rates were measured as changes in weight on a Mettler #10 analytical balance. Equilibration periods between readings were 1.5 hours. Copper-constantan (0.0076 cm diameter) thermocouples and a Fluke digital thermometer (2100A) were used to monitor air and leaf temperatures. A fan in each mini-chamber was run to prevent CO_2, O_2 and temperature stratification, and to reduce boundary layers. Measurements in the dark were taken using a flashlight with a green filter to prevent stomatal opening. Humidity within the large Controlled Environment Chamber (Chagrin Falls, Ohio) (CEC) was maintained at a constant 70% RH and 20°C temperature for the duration of the experiment. Finally, leaf resistance was calculated according to the Bot. 324-325 Lab. Man. 1980-1981. as:

$$RL = \frac{Csat - Cair}{TSP} \text{ s/cm}$$

where:

Csat = saturation at absolute humidty at leaf temp (°C)

Cair = absolute humidity of the air at air temperature

TSP = transpirational rate cm^2

with values for Csat in $/m^2$ taken from Slavik (1974).

Leaf Resistance (RL)

Leaves control approximately 99% of the transpirational water loss through their stomates (Meidner and Mansfield, 1968). RL for *Arctostaphylos uva-ursi* leaves was monitored in the field from sunrise to sunset, occassionally past it, once a month

throughout the growing season, from April to November to establish both a diurnal and a seasonal profile of water regulation.

A twig of *Arctostaphylos uva-ursi* was stemmed into terostat, a commercial sealant, and then inserted into the acrylic chamber of a Kanamasu aspirating diffusion porometer (Turner *et al.*, 1969). The time required for the humidity to rise to a predetermined amount within the chamber was recorded and the chamber temperature was noted. Leaf resistance was calculated differently than RL of VPD measurements according to Turner and Parlange (1970)(Appendix II).

Xylem pressure potentials (XPP)

Overall internal water status ( ) of the whole plant can be determined by measuring xylem tensions (Scholander *et al.* 1965). The values reflect the degree of water stress or value average turgor (VAT)(Tyree and Hammel, 1972)(see Appendix III) the plants are experiencing at the time of measurement, and are also directly related to the transpirational control (Hinckley *et al.* 1979, Ritchie and Hinckley, 1975), and probably have an affect on photosynthetic rates.

Xylem readings of cut twigs were taken in the field or in the lab with a pressure bomb (PMS, Corvallis, Oregon) and were measured in MPa. When immediate measurements could not be taken, the twigs were placed directly into tins lined with water-soaked paper towelling. This effectively produced a chamber with 100% RH which reduced transpirational losses and prevented changes in xylem tension values due to these losses. The pressure chamber itself was lined again with wet paper towelling against the desiccation of the arid N_2 gas on the leaf and twig tissue.

Pressure-Volume (P-V) Curves

The methodology used in constructing the pressure-volume curves is detailed in Cheung *et al.* (1975), Tyree and Hammel (1972) and in the original paper by Scholander *et al.* (1965). P-V curves can be used to determine cell wall elasticity. The model is discussed from a mathematical and philosophical view in Acock's equilibrium model (Acock, 1975).In producing a P-V curve reciprocal pressure (MPa) is plotted against volume of water, expressed as kg x 10^{6}, to yield a curve in the shape of a rectangular

hyperbola. Reflecting through internal changes in water potential ( ) the parameters , the bulk modulus of elasticity, n, the coefficient of non-linearity and can be derived (Appendix 11).

E. Photosynthetic Measures

Net Assimilation (NA)

NA is a measurement of the capacity of a plant to fix CO_2. At the biochemical level, NA differentiates between CO_2 respired and CO_2 fixed into sugars during photosynthesis. It was thought that a difference between the ploidy levels might be expected in their photosynthetic capabilities. Interpopulational differences were also examined between winter and summer (greenhouse grown) tissue.

Twigs were cut under water and then hydrated in the dark for 24 hours as in the pressure-volume (P-V) curve experiments. A twig with approximately 50 cm^2 leaf area was *cuvitized* into an open IRGA system (infrared gas analysis, Sestak *et al.* (1971). A constant airstream of 300 ml/min at an ambient concentration of 320 ppm gas was generated by a Kintek CO_2 permeation source (Texas City, Texas) and delivered over the leaf tissue. CO_2 uptake was recorded and calibrated on a Beckman 10" recorder (Arlington, Illinois). Quartz iodide and mercury vapour lamps within the walk-in CEC (Environmental Growth Chamber, Chagrin Falls, Ohio) were used in combination to vary light intensities to a maximum of 1800 $uE/m^2/s$ (almost full sunlight on a summer's day). Photon flux was recorded using a LICOR Quantum Light Integrating light sensor LI188. Cuvette air temperatures were maintained at 17°C using an array of controls (see the section on temperature response curves). Copper-constantan thermocouples (0.0076 cm diameter) were used to monitor both leaf and ambient temperature within the cuvette. A digital readout of leaf temperature was displayed on a Fluke 2100A digital thermometer. NA was calculated as:

NA = (C x F x Y x 273/Tl x 60)/LA (Bot. 324-325 Plant Physiol. Lab Man. 1980-1981)

where:

$C = CO_2$ assimilated (+) or respired (−) in ppm

$$Y = \frac{44 \times 10^{-6}}{22.414} \text{ (mg/ml)}$$

F = flow rate (ml/min at STP)

Tl = leaf temperature (K)

LA = leaf area (dm^2)

A simple porometer of Tygon tubing attached to a a 2 ml pipette attached to the twig enabled the concommitant measurement of transpiration. The final values of NA were plotted as a percentage of the maximum photosynthetic rate achieved in each experiment.

Temperature Responses

Temperature response measurements were performed at light saturation conditions for *Arctostaphylos uva-ursi* (1700uE/m^2/sec) to determine the photosynthetic response of chromosome races over a temperature range of 5−25°C. All temperature response curves were performed using a walk−in growth chamber (CEC) as a major source of temperature control. Other equipment included:

1. A water bath with continuously flowing cold water was placed between the light source and the cuvette with the depth of the water constant so as not to vary the wavelength intensities reaching the leaf tissue.
2. A Peltier cooling block (Thermoelectric 920) which was placed immediately below the cuvette.
3. A fan within the cuvette which insured an even mixture of the incoming and outflowing air and a reduced boundary layer.

Pigment Extraction

Traditionally, spectrophotometric assays of the reaction centers, chlorophylls a and b, are performed using an acetone extraction technique pioneered by Arnon (1949). Extraction of the pigments with DMSO has been noted to give comparable results but with greater speed (Hiscox and Israelstam, 1979, Shoaf and Lium, 1976). This method was used here, coupled with Kirk's (1968) nomogram to determine the the concentration values in ug/ml for both chlorophylls.

Approximately 10 ml of DMSO (analytical grade, Fisher) was added to each test tube and placed into a water bath at 55°C. Leaf discs 0.02 cm in diameter were punched out from both *young* leaves (current year's growth) and *old* leaves (previous year's growth) using a #2 borer. The discs were used to determine the dry and fresh weights of entire leaves. The leaves minus the disc were added to each test tube. Seven replications of both *young* and *old* leaves were made for each chlorophyll measurement. After 15 minutes in the water bath, the liquid levels were brought back up to volume, the extracts covered with a black light-tight cloth to minimize chlorophyll degredation and absorbancy was measured in the dark (green light filter) with a Unicam Spectrophotometer (SP1800) for the wavelengths of 645 and 663 nm for chlorophyll a and chlorophyll b respectively. Chlorophyll was expressed as a ratio of a/b, as a percentage of total chlorophyll/ug of dry weight of leaf tissue or as mg chlorophyll/mg dry weight tissue. Leaves were oven dried overnight at 70°C for determining the dry weight measures.

In solving for *x*, the following calculations were made:

1) g fresh wt./*x* g dry wt. = disc g fresh wt./ g disc dry wt.

2) nomogram reading (Kirk, 1968, ug/ml) x 10 ml/g dry wt. x 10^{3} = chl(x) mg/g dry wt.

III. RESULTS

A. Chromosome Determinations

The basic chromosome number within the family Ericaceae is x=13 (Grant, 1982, Stebbins, 1938). Diploid chromosome numbers in populations examined were 2n=26 and the tetraploid numbers were 2n=52. The identities based on taxonomy were thus validated (Table 1).

B. Water Relations

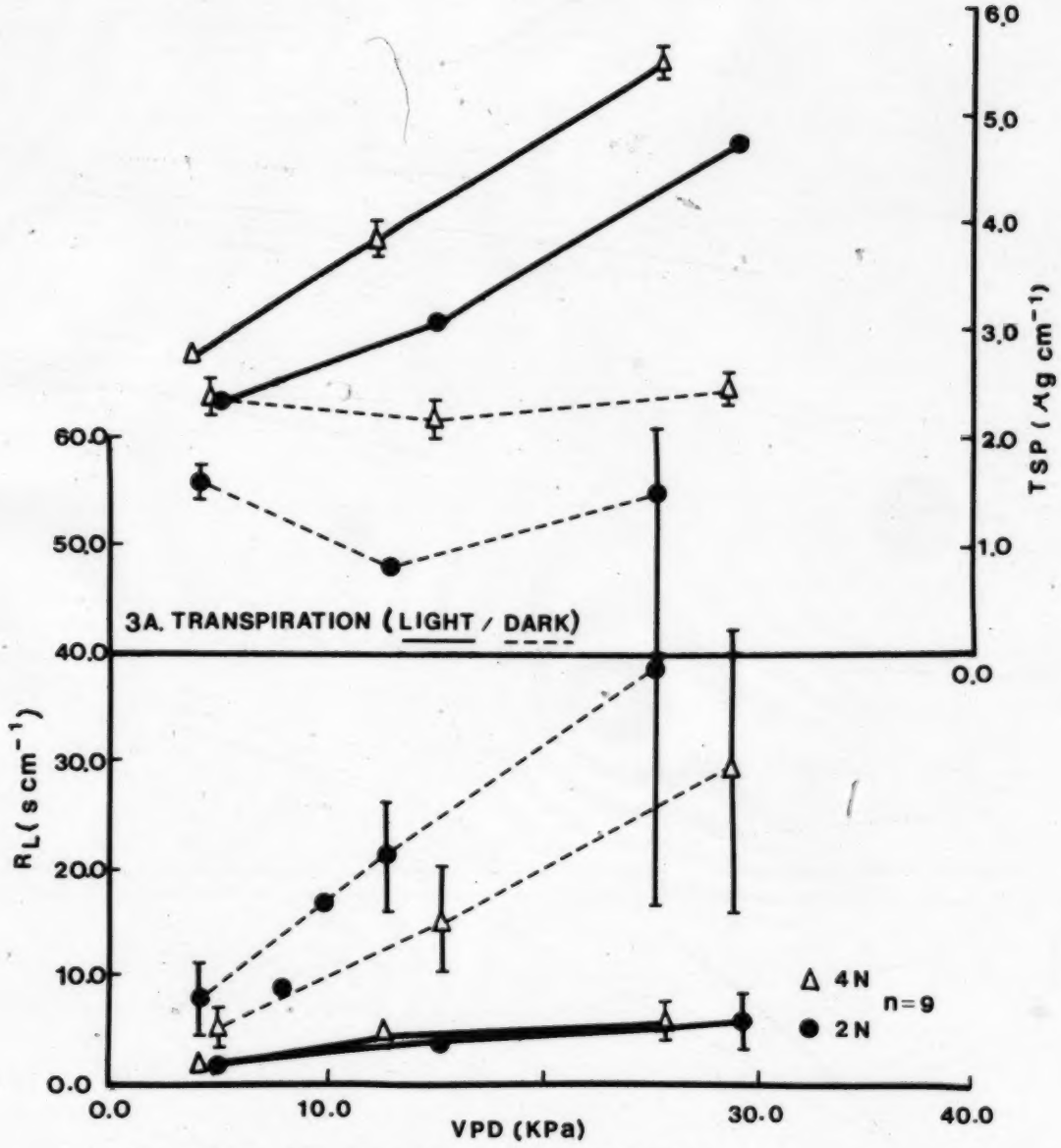
Whole plant transpiration (TSP), leaf resistances (RL), these parameters as they vary with vapour pressure deficiet (VPD), xylem pressure potential (XPP) and pressure-volume (P-V) curves were monitored in both the field and the laboratory following the phenological sequence of flowering to seed set and dormancy.

Leaf resistance (RL) and transpiration (TSP) responses of summer-type tissue to varying vapour pressure deficits (VPD) (Fig. 3)

Leaf resistance (RL) and transpiration rates (TSP) in the light respond inversely as humidity increases and are typically regulated by feedback (Sheriff, 1979) or feedforward responses (Farquar, 1978). These measurements were made under various VPD as reconnaissance tests to determine bearberry's response with humidity changes under complete hydration. Experimentally, this attribute of bearberry response freed the results obtained during the IRGA experiments from error in NA calculations incurred due to any fluctuation of humidity in the system.

RL of summer twigs of bearberry do not vary significantly from a mean of 5.0 s/cm across a 77% RH range (2.3bKPa)(Fig. 3). This is true for both ploidy levels. It implies that the feedback system of stomatal closure in these plants is not due to changes in ambient humidity as with many other species (Sheriff, 1979). For example, an orchid *Paphiopedilum leeanum* experienced a 274% increase in the TSP and a 6% increase in RL under the same ambient conditions (Mayo and Ehret, 1980). Closure for *Arctostaphylos uva-ursi* instead appears to be dictated by an internal water regime.

Figure 3. Behaviour of fully hydrated twigs under various vapour pressure deficits (VPD). Where SE did not exceed 0.5, SE bars were omitted. 4N tissue was from Ribbon Creek, 2N from Grizzly Creek. Both were greenhouse propogated.



3B. LEAF RESISTANCE (R_L)(LIGHT/DARK)

TSP rates for both ploidies increases as VPG increases between the leaf and the atmosphere (Fig. 3a). TSP rates are significantly higher (viz.) for the tetraploid and implies perhaps a facilitated gas exchange. Similarly, under controlled conditions in the dark, RL expectedly increases with increasing VPD (Fig 3b) but the increase in the diploid is greater than for the tetraploid, indicating that the diploid might have one or more of the following:

1. a higher cuticular resistance
2. a higher mesophyll resistance
3. 'tighter' stomatal closure.

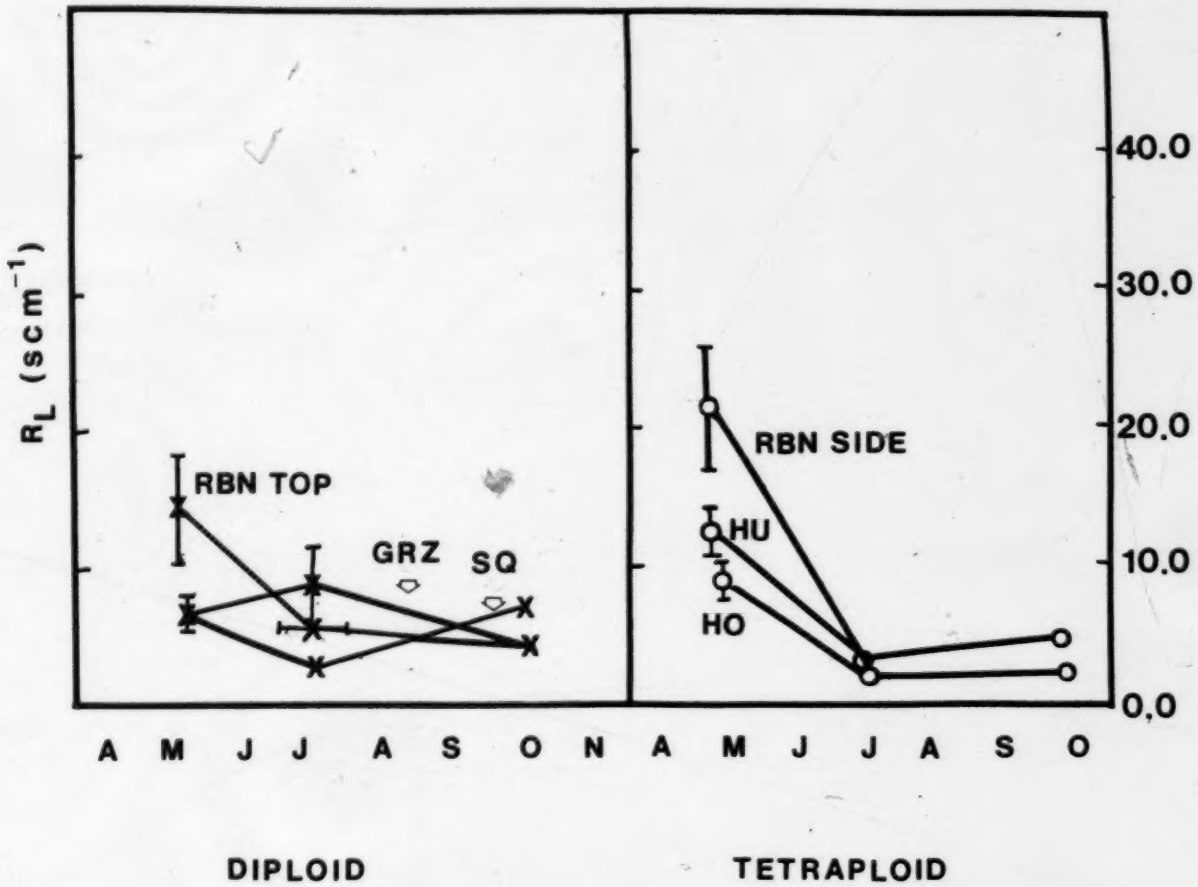
The tetraploid's high rate of TSP indicates that it is more vulnerable to decreases in and concomitant losses of turgor. this is in accord with the P–V data which show that the tetraploids would lose turgor more rapidly compared with the diploid with changes in bulk water status.

Laboratory value of RL agree in magnitude with summertime field values indicating that the treated twigs are behaving as they would *in situ*. One can confidently compare the two sets of data. Additionally and most importantly, since the plants used in gathering RL and TSP data were greenhouse grown for almost a year, the values reflect not just the plants adaptation to the experimental environment. The higher transpiration rate observed in the tetraploid are then, a direct result of ploidy.

Field seasonal pattern for minimum leaf resistance (RL) in young leaves (Fig 4)

For both ploidies, under subnivean conditions in November, the RLs measured were low (8–15 s/cm) indicating stomatal closure (not graphed). From May to June, RLs declined to a July (midsummer minimum) between 5–10 s/cm and then increased towards September as winter desiccation began. The pattern that the tetraploids show here are visibly distinct from the gradual decrease and increase that the diploids show. The tetraploids have a prominently lower minimum RL in July and it is important to note that the standard error bars here are also very low (0.5), those of the diploid are 0.5 and are more variable. Field minimum RL in the summer is in good accord with the values of RL obtained in the summer from fully hydrated green house material of Fig. 3. Under field conditions, the diploid values are never as low as the ones obtained under laboratory conditions This indicates that the diploid is possibly not as efficient in its water uptake despite its more

Fig. 4. FIELD MINIMUM LEAF RESISTANCE (R_L) in YOUNG LEAVES of ARCTOSTAPHYLOS UVA-URSI during a growth season/1980.



Minimum R_L values were measured at dawn. They represent fully hydrated tissues. For every value plotted, n = 7. The standard error bars, where they are very low, <0.5, are omitted. This occurs in the tetraploid data, while R_L for the diploid are highly variable.

mesic environment.

Seasonal shift and diurnal rhythm in xylem pressure potential (XPP) in field populations (Table 2, Figs. 5 and 6)

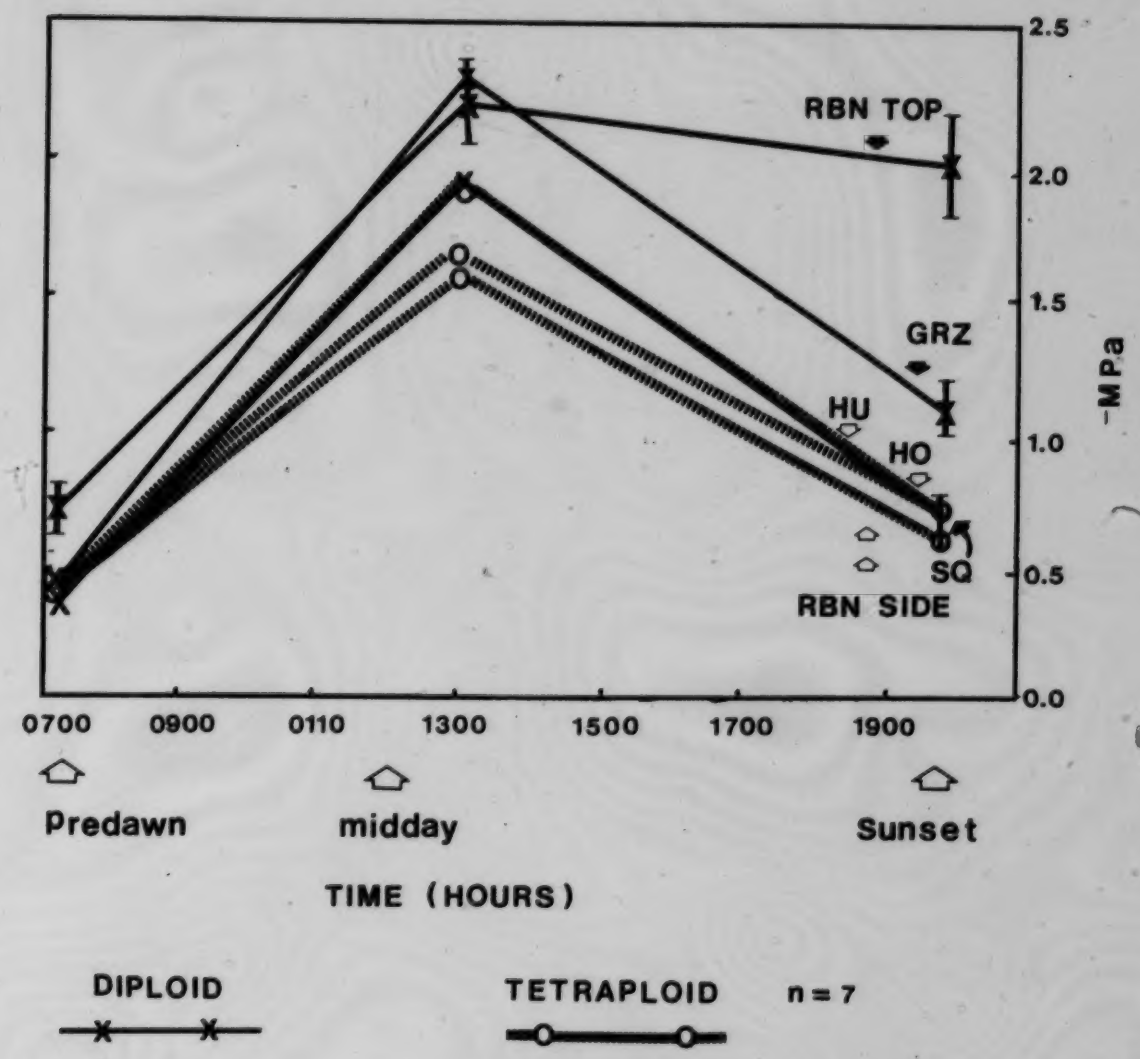
XPP is a measure of the water status of a plant. As a balancing pressure (bp) or XPP at a particular Ve, it measures the of the tissue (Helkvist *et al.* 1974, Ritchie and Hinckley, 1975, Tyree *et al.* 1973). It has a wide ecological application in assessing the degree of water stress due to transpiration/photosynthesis (Ritchie *et al.* 1975, Cheung *et al.* 1975), drought (Hinckley *et al.* 1980, Kandiko *et al.* 1979), and membrane damage (Turner, 1976). For this study, the relative XPP of two ploidy levels of *Arctostaphylos uva-ursi* were monitored with the intent of observing water stress and *content* – , from April through November, *i.e.* from a period of dormancy where subnivean XPP is high (−2.5 MPa) and the twigs are essentially dessicated . Grizzly Creek (Table 2) is the only population with a significantly lower spring XPP (−0.9 MPa). This population was most exposed at the time of reading in the late winter and was resaturating from a nearby runoff channel of water. Thus, dormancy release and a return to a normal water budget appeared earlier in this population. The subnivean values are unlike winter XPP for *Pinus contorta* of −0.7 MPa (J. Mayo pers. comm.) which forms the overstory of the community. A XPP of −2.5 MPa is a relatively low value for bearberry. In fact, it seldom exceeds this value in midday throughout the growing season. During spring resaturation of woody and leaf tissue reaches saturating conditions or low (0−0.5 MPa) from available ground water. The diurnal summer pattern is one of low, high and low XPP followed by a fall antithetic desiccation where tissues were so dry that XPP as low as −6.0 MPa were recorded (not graphed). This desiccation is likely an avoidance mechanism against intracellular ice damage. In midsummer the dipoid experiences a higher daytime stress than the tetrploid (Fig. 5). This is surprising since the diploid is essentially in a more highly buffered and moderated environmental setting. Initially it was thought that the trends observed were a consequence of the local water availability. But P−V curves and photosynthetic responses support the idea that the tetraploid perceives the stress more quickly. Its strategy is to 'slam shut the stomates'; hence the observed higher XPP at midday, while the diploid, perhaps due to its abundant water availability, reacts more sluggishly re. stomatal closure.

TABLE 2. SUBNIVEAL XYLEM PRESSURE POTENTIALS (XPP)

DIPLOID	XPP (-MPa)	TETRAPLOID	XPP (-MPa)
Grizzly Creek	0.91	Hill Open	2.10
Squirrel	2.73	Hill Under	2.53
Ribbon CrkTop	2.52	Ribbon Crk	2.52

XPP Readings were taken in the field in April 1980

Fig. 5. PATTERN of XPP (-MPa) on a MIDSUMMER'S DAY



SE bars are omitted purposely when the values are less than 0.5.
The date of sampling was July 26, 1980.

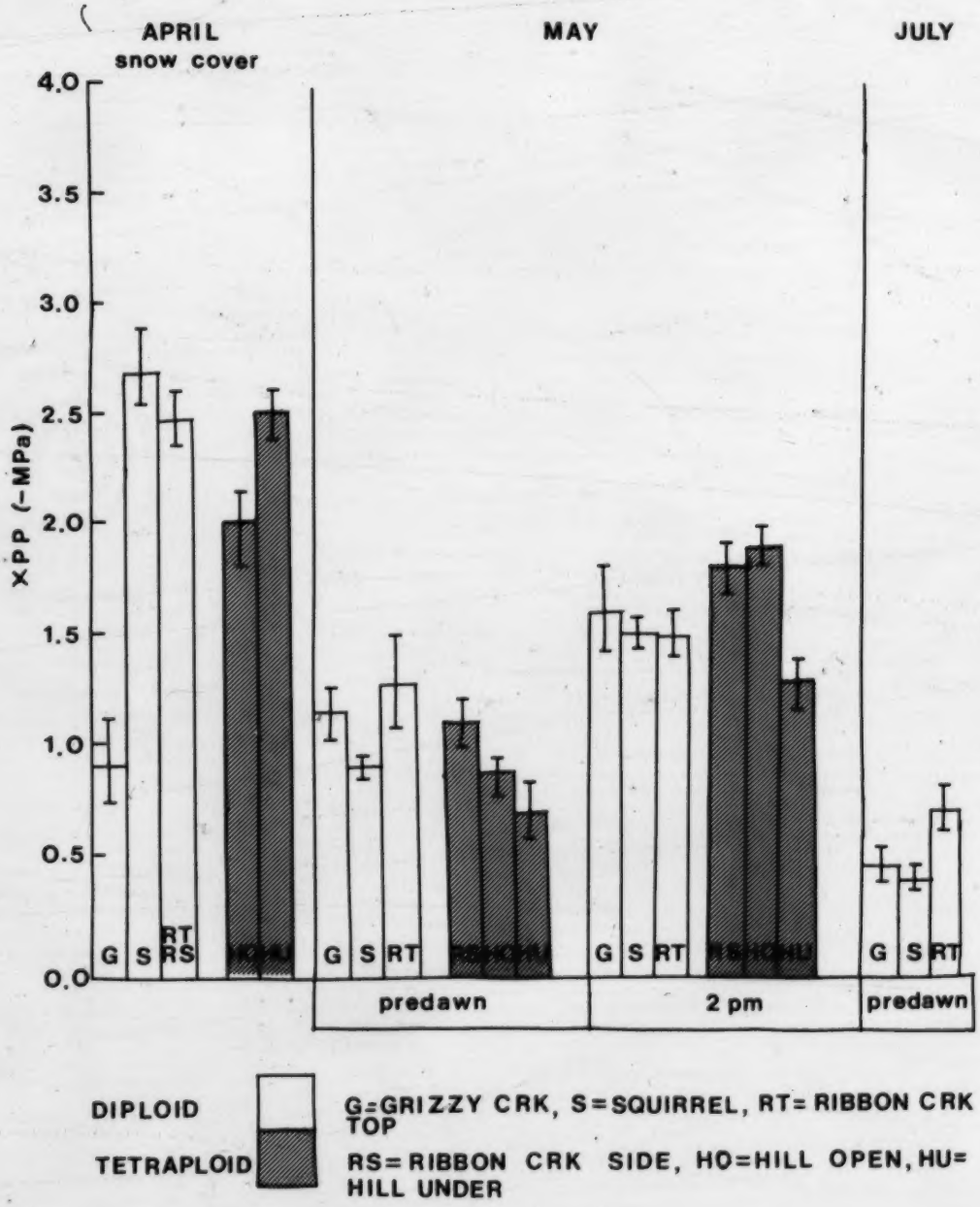
However, the diploid may appear to experience a higher stress when, in fact, it might have a higher threshold of closure due to water loss. Again this might be attributed to the more elastic cell walls

Returning to the summer on a single day in July (Fig. 5), the XPP pattern is one of low XPP (−0.5 MPa) for both populations at predawn. Values rise to a midday maximum XPP (ca. −2.5 MPa) where water stress is a maximum, where the VPG between atmosphere and leaf becomes the highest, and the concommitant physiological reaction is a midday stomatal closure (Meidner and Mansfield, 1968). A return trend is to a low morning XPP as the plants replenish their water supply.

The differences between the ploidy levels become accentuated under stress toward the summer's end as the tissues prepare for winter. Amplitudes and rhythms become exaggerated and desynchronize from the summer patterns (Fig. 6). By October and November, both races appear to be more water stressed in the morning, *i.e.* the previous low summer XPPs are not being achieved. Predawn values are approaching 2.0 MPa, an indication that the stomates are opening or remaining open during the night and transpiring water as part of the winter hardening strategy. A similar desiccation tactic has been noted for another ericaceous shrub, *Ledum groenlandicum* (Wilkinson, 1977). The amplitude differences decrease between the noonday, predawn and night readings as the plants move into a wintering condition. By November, the diploid's ranges of daily fluctuations are more errattic and indicate that they have less control over their stomates. The polyploids are behaving much more modestly in their fluctuations between midday and sundown. This hints at a higher cold tolerance of the tetraploid over the diploid. The stomates function normally despite the colder night temperatures and the greater difference between the night and daytime temperatures. It appears that the tetraploid entities have more bulk water control and are more stable than the diploids despite their more unstable environment and can extend their growth period farther into the season.

Fig. 7 compares a midsummer XPP of the tetraploid populations HO and HU which are both tetraploid, *i.e.* bearberry from an open and from a closed community under a *Pinus contorta* overstory, after a summer rainshower. Indications are that bearberry from the open environment has the capacity to serendipitously absorb water in a space of time as short as 15 minutes. Initially, XPP for the exposed populations are higher, indicating a

Figure 6. Seasonal shift in xylem tension within the 6 populations. Readings are at predawn and midday. Key: 6 = Grizzly Creek, S = squirrel, RT = Ribbon Creek Top, (2N). RS = Ribbon Creek Side, HO = Hill Open, HU = Hill Under, (4N).


APRIL
snow cover
MAY
JULY
4.0
3.5
3.0
2.5
2.0
1.5
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0.5
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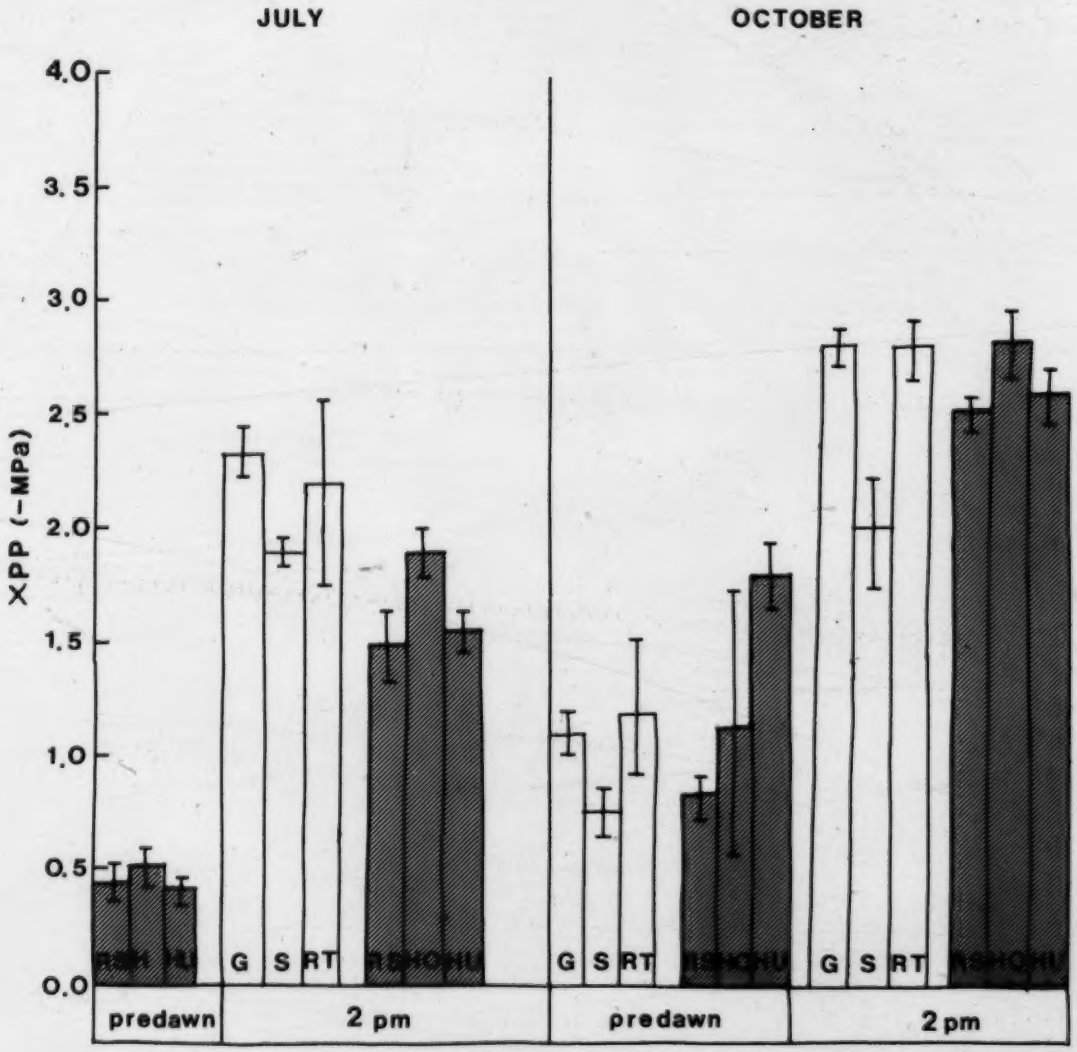
XPP (-MPa)
G
S
RT
RS
HO
HU
predawn
2 pm
DIPLOID
TETRAPLOID
G=GRIZZY CRK, S=SQUIRREL, RT= RIBBON CRK TOP
RS= RIBBON CRK SIDE, HO=HILL OPEN, HU= HILL UNDER


JULY
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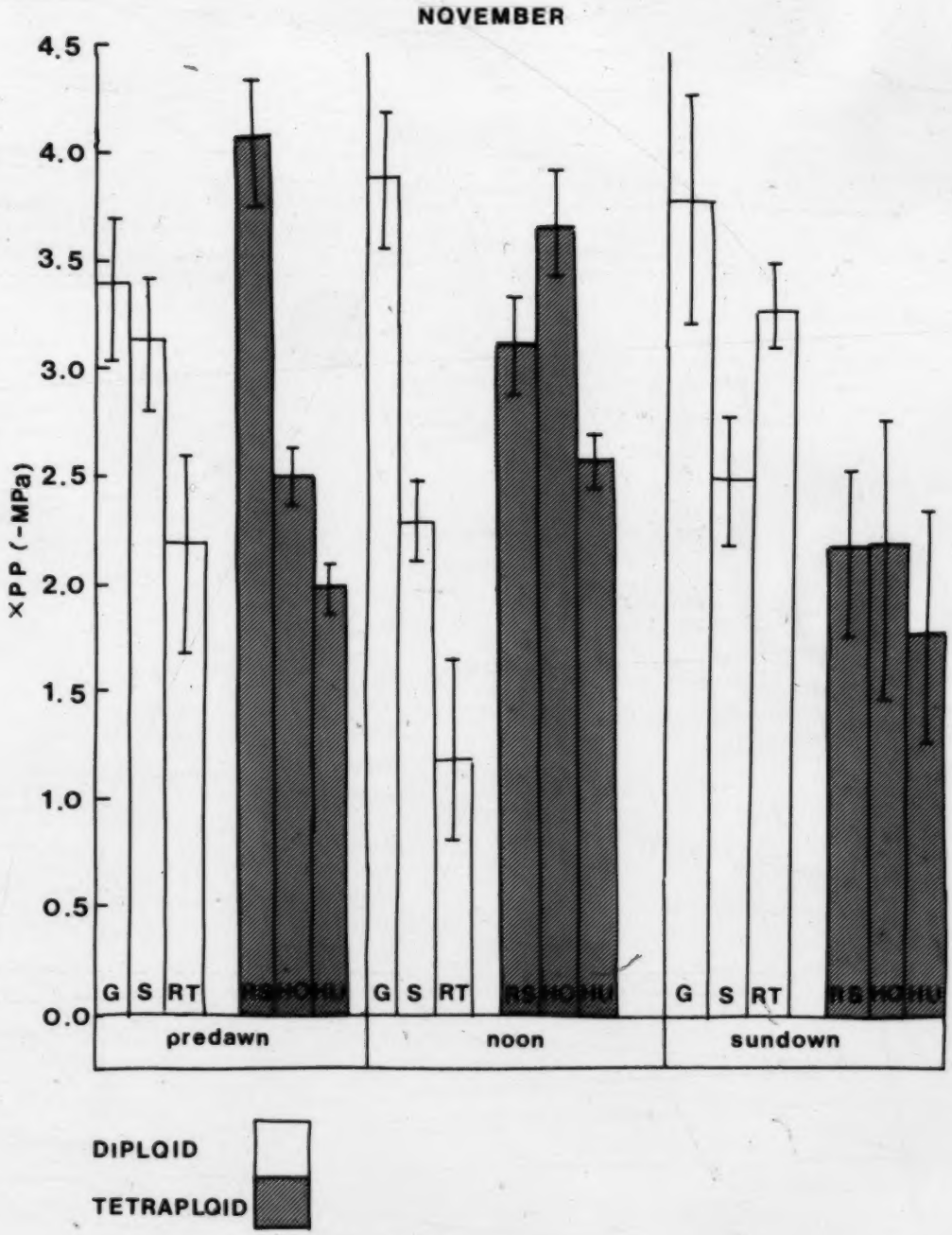
NOVEMBER
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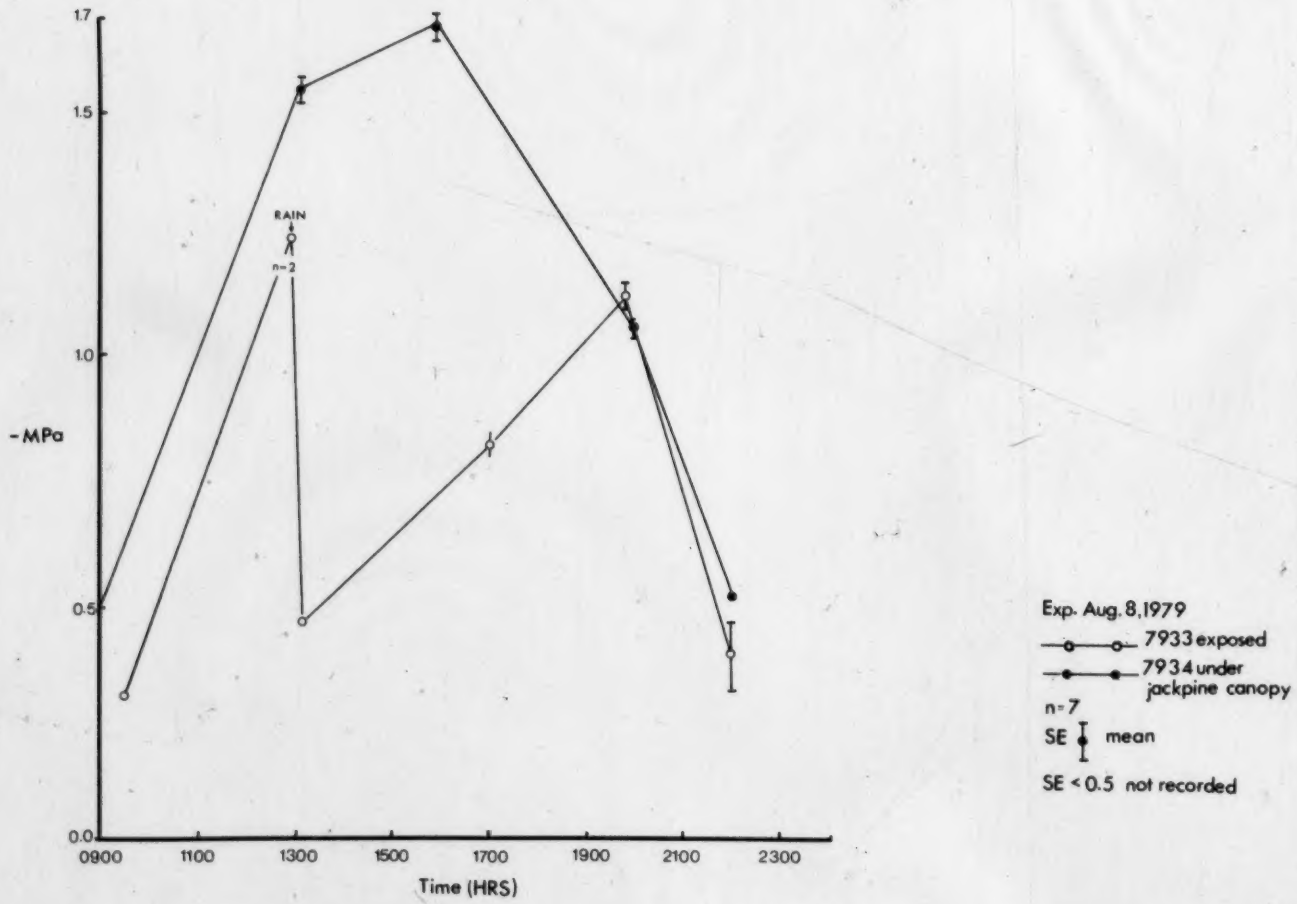
2.5
2.0
1.5
1.0
0.5
0.0
XPP (-MPa)
G
S
RT
predawn
noon
sundown
DIPLOID
TETRAPLOID

Fig. 7 Field Xylem Pressure Potential (-MPa) for ARCTOSTAPHYLOS (4N) at the Hillside Station Kananaskis Valley, Alta.



'less stressed condition' even though the environment is seemingly more exposed and more stressful than the shaded one. It might be that the root resistance is so low that the plant is able to resaturate quickly to low XPP (1.0 MPa).

The environmental influence is important in determining the extremes in which the tetraploid bearberry is examined. In an exposed environment, tetraploid bearberry is an opportunist and has the capability to maximize whimsical summer and fall rain; maintain a lower XPP at midday in midsummer and to extend its 'summer' past the diploid's which begins it's winter desiccation.

Pressure-Volume (P-V) Curves (Fig.8, Table 3)

A rheological definition of elasticity of the cell walls is as a stress/strain ratio (Scott Blair, 1969). This is the ε, comparable also to Warren Wilson's coefficient of enlargement (1967a and b). A high ε value thus implies a rigid cell wall and a low ε, an elastic one.

Other values which may be derived from P-V analyses include:

1. π_0: the osmotic potential of the cell which relates to the symplastic contents. It is one of the components, along with ε, which determines the rate of turgor loss, the πp point, and the limits of VAT that the tissue can potentially experience.
2. πp: the osmotic potential at incipient plasmolysis. The higher the πp, the lower the limit at which positive turgor exists and its magnitude depends on πo and
3. VAT: Value Average Turgor, decreasing turgor at any given Ψ stress before incipient plasmolysis.

Since midsummer appears to be the time at which physiological differences between the ploidies are maximal, it will be the primary focus of attention, although some seasonal aspects will be considered. Winter hardened tissues were compared with summer type tissue for both ploidies. Diploid and tetraploid winter tissues have similar absolute values of ε (Table 3) and these are perhaps indicative of a genetic *status quo, i.e.* there is no physiological gain here for the tetraploid by having an increased genome. It may be that under winter conditions ε is not a useful differentiating character or that bearberry has evolved the 'best' or optimal winter desiccation survival strategy as far as the distribution of symplastic and apoplastic water and it is not 'changing' evolutionarily or that if changes

of its expression are still occurring, it is not as yet manifest between the races.

The most important differences in the behaviour of the two ploidy levels occur when the cells are physiologically active. From winter to spring and summer, bearberry undergoes qualitative changes in the cell walls which make the tissue less elastic and more rigid (ε values increase).

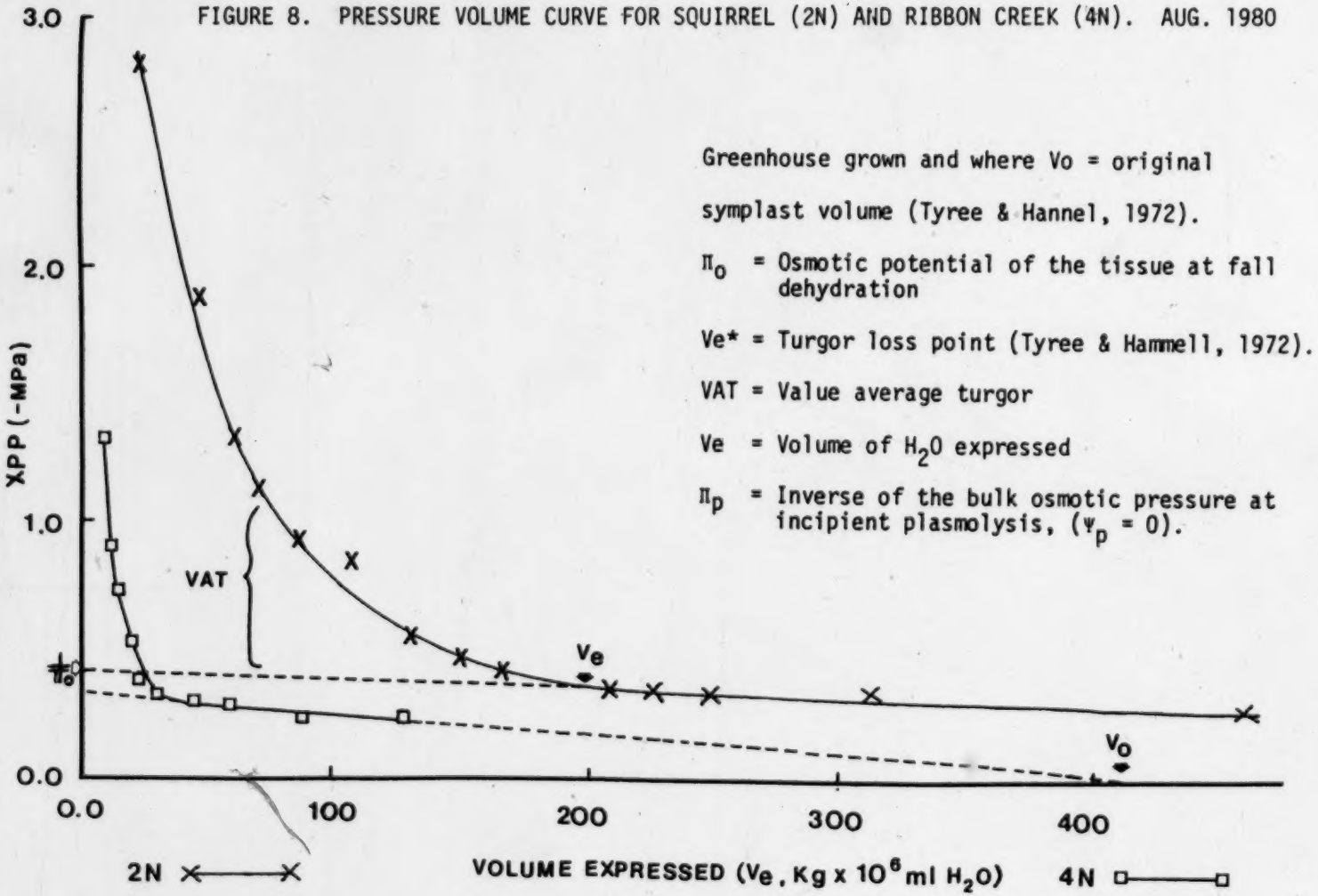
Winter ε's are lower than those for physiologically active summer tissue by one or even two orders of logarithmic magnitude, *e.g.* 9.0×10^0 (4n) and 9.0×10^1 (2n) for winter tissue compared with 3.2×10^2 (4n) and 5.6×10^2 (2n) for summer tissue. Winter wood is 'softer' than summer wood. This can provide a baseline for viewing the magnitude of the shift in cell wall 'camber' between seasons and enable one to judge the phenological state of the tissue.

Two P–V curves for August tissue over a range of balancing pressures of 0.5 to 3.0 MPa (Fig. 8) demonstrate that the diploid tends toward a lower and slower perception of turgor loss. Several factors contribute to this:

1. water content in the diploid is appreciably higher (Vo=900 kg x 10^6 ml) compared to the tetraploid (380 kg x 10^6 ml).
2. value of the diploid is 1.6×10^0 MPa compared to 2.2×10^2 MPa of the tetraploid (Table 3). Rigidity of the cell wall in the tetraploid is evident, as elasticity is for the diploid.

The diploid is the more highly 'hydrated' of the twigs. The Vx (volume of apoplastic and symplastic water before incipient plasmolysis is reached) is not dependent directly, in this case, on ε since the diploid and tetraploid have comparable values, −2.5 and −2.6 MPa respectively, or on Πp since it is −2.9 MPa for both. Thus it is, that high Vo coupled with low ε, and not Πo or Πp, enables the cell walls of the diploid to osmoregulate and accomodate turgor pressure changes over a wider range of turgor drop. In the terminology of Walter (1931), the diploid is *hydrolabile*. Small changes in the RWC, result in a rapid loss of turgor for the tetraploid. It has less extracellular water to lose before symplastic water begins to be drawn from the cells under a water stress. The tetraploid, in Walter's (1931) terminology, is *hydrostable*. Any loss of turgor is rapid because of rigid cell walls. It is likely that the diploid is able to continue photosynthesis over a wider range of low Ψ stress, while the tetraploid is not able to do the same. In fact,

FIGURE 8. PRESSURE VOLUME CURVE FOR SQUIRREL (2N) AND RIBBON CREEK (4N). AUG. 1980



Greenhouse grown and where Vo = original symplast volume (Tyree & Hannel, 1972).

π_o = Osmotic potential of the tissue at fall dehydration

Ve* = Turgor loss point (Tyree & Hammell, 1972).

VAT = Value average turgor

Ve = Volume of H_2O expressed

π_p = Inverse of the bulk osmotic pressure at incipient plasmolysis, (Ψ_p = 0).

Table 3. A comparison of cell wall rigidity between winter hardened and summer tissue. Both ploidy levels are represented. Parameters examined are ε, the bulk modulus of elasticity and n, the coefficient of non-linearity.

Source and phenology	4N ε (MPa)	4N n	2N ε (MPa)	2N n	Site
Winter hardened tissue, Nov. 23/81					
Ribbon side	2.8×10^{-1}	1.6	2.3×10^{0}	3.3	Ribbon top
Hill under	9.0×10^{0}	8.5	9.0×10^{-1}	0.5	Squirrel
Hill open	3.2×10^{0}	2.8	1.3×10^{0}	39.5	Grizzly Creek
Summer tissue, 1980					
Rbnside with flowers, Mar. 14	3.2×10^{2}	6.0	5.8×10^{2}	5.6	GRZ Crk Mar. 9
Rbnside, May	2.0×10^{3}	3.1	-	-	-
Rbnside, veg. only, July 6	6.5×10^{0}	5.6	2.6×10^{3}	41.6	GRZ Crk July 7
Rbnside, Aug. 18	2.2×10^{2}	2.4	1.6×10^{0}	4.4	SQ Aug. 15

Values of ε and n are derived from P-V curves from a log-log plot of VAT (MPa) vs $\frac{V-Vp}{Vp}$ (relative volume (kg X 10^6). ε is the bulk modulus of elasticity and indicates how rigid the cell wall is, i.e. how it responds to losses of turgor pressure and n is the coefficient of linearity. The greater the value of ε is the more rigid is the cell wall.

Note: that a seasonal survey represents a slightly novel approach to P-V curve analysis when compared to the usual point-comparisons made between species in Tyree and Hammel (1971).

turgor loss point has been linked with a threshold of stomatal closure (Hinckley, 1980) which would mean a halt of photosynthesis under a situation where the tetraploid perceived a water stress.

Seasonal variation in ε and **n** (Table 3)

Although midsummer is the point in the growing season during which the differences between the races seem maximized, there appear shifts to other polarities for ε and n values for both ploidies. On July 6, the tetraploid *Ribbon Side* had an ε value of 6.5×10^{0} and the diploid *Grizzly Creek* had an ε of 2.6×10^{3}. The tetraploid appears to be less rigid in its cell wall properties and more elastic in the summer, the diploid appears more rigid in midsummer. By August, the situation seems to have reversed itself and the tetraploid appeared to be more rigid, its ε being 2.2×10^{2} and the diploid is becoming more elastic, its ε values at 1.6×10^{0}, similar to those of winterized tissues. The present data do indicate that a seasonal shift of the elastic properties of the cell wall does occur from being relatively rigid in the summer to elastic in the winter. In summer, the diploid has more elastic cell walls, and the *times* at which these physiological changes which alter the properties of the cell wall occur, vary with the ploidy level.

Seasonal Shifts in Πp and Π_0 (Table 4)

With rigid cell walls, the difference between Π_0 and Πp is small (Cheung *et al.* 1975. The greatest difference between them occurs between the diploid and the tetraploid winter values. Winter diploid tissue has differences ($\Pi_0 - \Pi p$ of 3.57, 1.1 and 3.8 MPa, while winter tetraploid has difference values of 0.8, 1.0 and 1.7 MPa. Winter diploid tissue, relative to the tetraploid, is more elastic. This is in agreement with the observations of Mazur (1969), but is in contrast to the increase in rigidity during tissue hardening observed in *Ledum groenlandicum* (Wilkinson, 1977), spruce and pine trees (Jarvis and Jarvis, 1963), and other species (Parker, 1963).

In the summer, Π_0 increases for both ploidies as osmotic adjustments are made within the cell. These are likely to be the result of an increase of osmoticum due cellular activity related to cell elongation, regeneration and photosynthesis. The issue of increasing cellular solutes as cryoprotectants does not seem probable

Table 4. Seasonal changes in osmotic potential Πo and turgor pressure Πp at incipient plasmolysis for 4 and 2N winter and summer tissue. Πp and Πo are extrapolated values from P-V curves (Cheung et al., 1975).

Site	Πo	Πp	Πo	Πp	Site
Winter values, (-MPa) Nov. 23/81	(4N)		(2N)		
Hill open	1.2	2.0	1.43	4.0	SQ
Hill under	1.5	2.5	1.2	3.3	GRZ
Ribbonside	0.8	2.5	1.2	5.0	Rbn top
Summer values, (-MPa) 1980					
Ribbonside (May 23)	1.5	1.6	-	-	-
Ribbonside (July 6)	1.9	2.0	2.0	2.1	GRZ July
Ribbonside (Aug. 17)	2.6	2.9	2.5	2.9	SQ Aug.15

Key:

SQ = Squirrel
GRZ = Grizzly Creek
Rbntop = Ribbon top

as a winterizing mechanism in *Arctostaphylos uva-ursi* as π_0, in fact, decreases in winter from summer values.

In summary:

1. In summer, both ploidy levels have relatively rigid cell walls and the osmotic and turgor components are similar. The value at which VAT=0, *i.e.* bulk incipient plasmolysis is the same for both ploidy levels. ε changes without concommitant changes in π_0 or πp parameters, confirming that the changes in elastic properties are in the cell walls.

The nature of increased diploid elasticity may be due possibly to a change in the chemistry of cell membranes, *e.g.* lipid composition or a change from single to double bonds in existing molecules.

2. Vo summer values are greater than Vo winter values as seen from the previous graphs and indicate that water in summer tissue is osmotically and matrically bound.
3. In summer, water content is quantitatively higher in the diploid than in the tetraploid, indicating that most of it is apoplastic.
4. The tetraploid increases in π_0 from winter to summer, similarly for the diploid. π_0 is the highest when the plants are at a physiological optimum; increasing cellular osmoticum is not a mechanism for winter tolerance.
5. Tetraploid cell walls are less elastic than diploid cell walls.

C. Photosynthetic Measures

Net assimilation (NA) was compared between the chromosome races. Monitoring the NA capacity was the most manna'foid area for measuring the physiological variability between the two ploidy levels of bearberry. It provided a nexus to the many sublevels of investigation, *e.g.* the chlorophyll assays, another examination of transpirational control, seasonal profiles of photosynthetic enzyme efficiency as well as generating source material for pressure-volume and resaturation curves (not included in this section). The following parameters were obtained or calculated as a result; transpiration :TSP, Km and Vmax, light compensation points :LCP, and dark respiration rates :DR. The seasonal optimum temperature for NA was also monitored and the data treated by an Arrhenius plot of log NA vs leaf temperature as well as a log TSP rate vs leaf temperature. On the

Figure 9. Ribbon Creek (4N) and squirrel (2N) populations: Transpiration and light response curves. The maximum differences between the chromosome races are evident in NA and TSP in late summer (Aug., 1980). Samples were GH grown and n = 1.

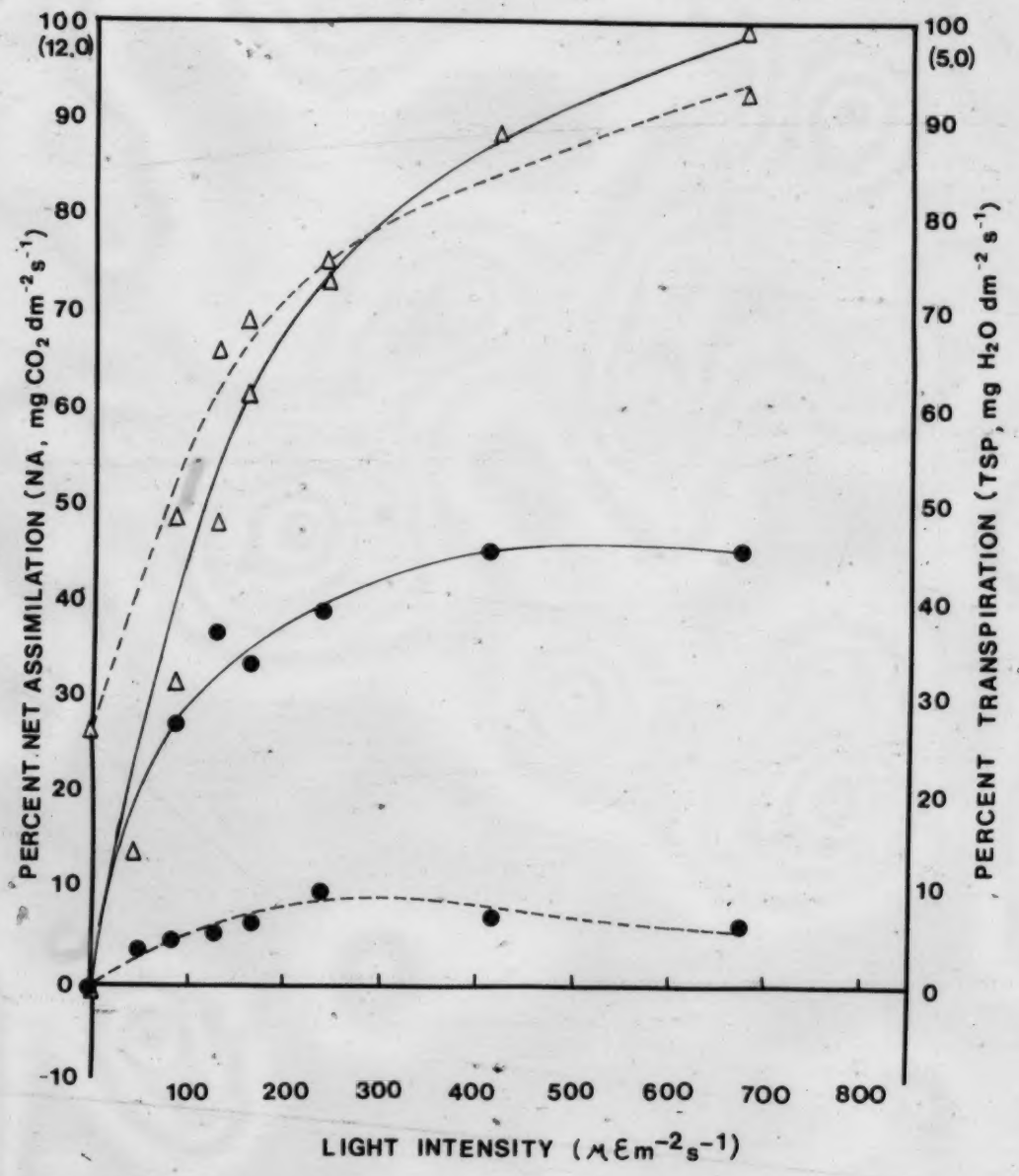
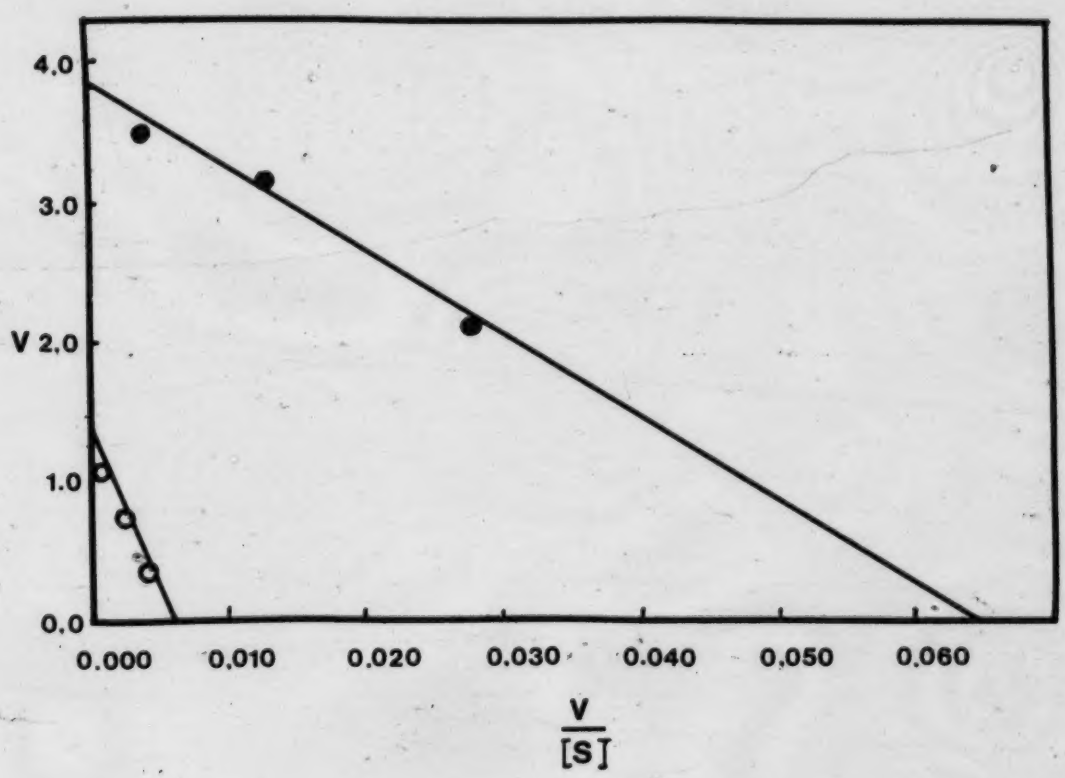

100
(12.0)
90
80
70
60
50
40
30
20
10
0
-10
PERCENT NET ASSIMILATION (NA, mg CO_2 $dm^{-2}s^{-1}$)
100
(5.0)
90
80
70
60
50
40
30
20
10
0
PERCENT TRANSPIRATION (TSP, mg H_2O $dm^{-2}s^{-1}$)
100
200
300
400
500
600
700
800
LIGHT INTENSITY ($\mu E m^{-2}s^{-1}$)

Fig. 10. Derivation of Km and Vmax from an Eadie-Hofstee transformation of a NA curve.



An Eadie-Hofstee plot of V (mg CO_2 $dm^{-2}h^{-1}$) or NA rate vs V divided by substrate concentration in light intensity $\mu\xi m^{-2}s^{-1}$. This is a transformation of Michaelis-Menton type NA curve where NA is plotted against light intensity. The graph is based on data collected from Apr. 14 - greenhouse grown summer tissue of diploid (2N) and tetraploid (4N) origin. Parameters Km are derived from the slope of the line, (m) and Vmax from the y intercept.

biochemical level a chlorophyll assay was initiated to determine if there were qualitative and/or quantitative changes throughout the season.

NA runs were conducted throughout the natural growing season with the cornerstone results shown in Fig. 9 for August tissue. The highest significance in differences of NA between the two chromosome races is recorded here. The photosynthetic maximum of the tetraploids was almost 150% higher (11.0 mg $CO_2/dm^2/hr$) than the diploid (4.0 mg $CO_2/dm^2/hr$). Light saturation occurred at a lower light intensity for the diploid – appropriate to its understory niche at 250 ue/m^2/sec. The tetraploid did not appear to be saturated at 350 uE/m^2/s indicating the ability of the *Ribbon Creek* tetraploid population to utilize the higher levels of irradiance and it is concordant with the exposed habitat that the tetraploids tend to occupy.

Transpiration rates concomitant with photosynthesis were also higher in the tetraploid which might indicate a higher water use efficiency by the tetraploid. The results are shown in Table 6 for ease of comparison.

A stomatal index (SI, Meidner and Mansfield, 1968) (Appendix III) was calculated to explain the doubled NA, higher TSP rates and lower RL of the tetraploid. The tetraploid had an SI of 5.66%, *i.e.* 59 stomates/mm^2 and the diploid had an SI of 5.49% or 68 stomates/mm^2. Within a range of +20 or −20 stomates/mm^2, the differences counted are insignificant. It is concluded that stomatal density *per se* has little or no bearing on an enhanced gas exchange ability of the tetraploid.

Seasonal NA, Vmax and Km (Table 5)

The value of Km is defined as the substrate concentration, in this case light energy, at which the rate of reaction is half of the Vmax or half of the maximum photosynthetic rate. When Km is high, there is a low affinity of an enzyme for its substrate. When Km is low, there is a higher affinity.

The sequence in Table 5 indicates that bearberry's Km and Vmax values alter significantly with the time of the year. The diploid maintains a seasonally lower Km and would, by definition, have a higher affinity for the substrate of photosynthesis. Concurrently, tetraploid, Km values are equal to or higher than those of the diploid, especially by midsummer (237 *vs.* 154). This presupposes that the tetraploid will have a

Table 5. Seasonal shift of photosynthetic temperature optima (°C), Km and Vmax in diploid and tetraploid populations of *Arctostaphylos*, 1981.

Phenology	Source	°C		Km		Vmax mg CO_2 $dm^{-1}h^{-1}$	
		4N	2N	4N	2N	4N	2N
Spring							
Preflowering	GH	22.5	18	38*	59	3.62	1.50
Post flowering	GHR	20.0	-	114*	-	3.60	-
Post flowering	F	-	19	-	94*	-	3.68
Summer	GHR	16.0	14	237	154	3.30	3.30
Late summer	GH	ND	ND	124	60	11.30	5.60

n = 1 for all cases

ND = not determined, data from 1980

Preflowering 4N *Arctostaphylos* was collected from the field (recently snow-freed); diploid material in the same phenological state (F) was collected on Apr. 14. Post flowering spring tissue was sampled on Apr. 14 from GHR. Summer material was sampled for both of the chromosome races on two occasions, on May 12 and later on Aug. 14.
Kms derived via the Lineweaver-Burke transformations are indicated with an asterisk (*). When these yielded low r^2 values (<0.48) an Eadie-Hofstee transformation was applied to obtain reasonable Km's & Vmax's.

Key:

F: field material (Kananaskis)
GH: greenhouse grown
GHR: greenhouse roof grown

less efficient CO_2 fixing ability. It does not take into account the light intensities encounterd in their respective environments–high for the tetraploids and shaded or low for the diploids. However light saturation occurs for the 2N and 4N at approximately 300 $m^{-2}s^{-1}$ so that an explanation for the tetraploid's superior (twice as high) NA rate (Fig. 9) for midsummer type tissue must be sought elsewhere. It is not due to differential RL as has been seen, but perhaps may result from a combination of:

1. increased chlorophyll b levels, *e.g.* the ability of tetraploid bearberry to utilize light quanta over an extended light range, (to be presented)
2. a lower resistance in the pathway of gas exchanges as evidenced by the high 4N TSP rates despite lower XPP,
3. an ability to utilize an opportunistic water supply, ground water fluctuation, and sensitivity to bulk internal water balance (rigid cell walls), which locks the tetraploid into a pattern of an early midday stomatal closure to conserve water.

The effects of all these components and the complimentary seasonal shifts in temperature optimum and light compensation levels, and possibly change in carbon partitioning, become very important on a daily and cumulative basis ultimately giving the 4N an overall advantage i.e a higher NA.

At the end of the growth season NA is greater for the tetraploid than for the diploid. This may be 'real' indicating that the tetraploid has an optimal time during the growth season where photosynthesis becomes more efficient or that its carbon partitioning demand is diverted towards winter carbohydrate storage or a second fall flowering. The diploid undergoes a slight increase. Possibly, the tetraploid perceives a seasonal change, while the diploid perceives less of a difference or is unable to utilize the environmental changes of shortened daylength, cooler diurnal temperature extremes and warm days of fall.

For both ploidies, Km is lowest and almost equal in the spring. After flowering, Km rises, NA remains the same but by midsummer, the differences in Km and Vmax are maximal (11.3 *vs.* 5.6) by midsummer.

A detailed Evaluation of NA Responses in Relation to Phenology and Chronology for LCP, TSP and DR (Table 6)

Spring

Figs. a and b (Appendix 111) show the NA curves for the time span between early spring and late spring and Table 6 summarizes them for LCP, TSP and DR. Phenologically, the time encompasses pre- and post-flowering periods.

Dark respiration appears higher (more negative) for the tetraploid (50% less for the diploid). The transpiration rate for the tetraploid is 80% greater than for the diploid. These two factors indicate a facile gas exchange capacity for the tetraploid but may also point to an inefficiency or energy utilized due to high dark respiration as the tetraploid repairs winter damage or instigates new vegetative and flower bud growth. The net effect in the tetraploid would be to depress NA from its potential maximum. The preflowering light compensation point is slightly decreased in the tetraploid – a possible adaptation to a low light intensity environment and may be especially important during a 'spring renovation' in maximizing available sunlight. For the diploid LCP is relatively high perhaps and this may relate to an environment in which there is almost no shade from the canopy of the deciduous overstory. As the season progresses, diploid LCP seems more labile and it decreases. This overlaps with and includes the after-flowering period of F and GHR material.

Early Summer (Preflowering)

Dark respiration rates are approximately equal, but the NA of the tetraploid is much higher (Table 5). A lower Km for the tetraploid indicates traditionally a greater affinity of the photosynthetic enzymes for CO_2. The overall result is a greater NA for the tetraploid. Transpiration rates are higher for the tetraploid than for the diploid but are not as elevated as they are in the spring. This could be due to a tighter water budget of the tetraploid or simply mirror an adjustment to a lower water availability once spring melt is over.

The maximum temperature for the optimal photosynthetic rate seemed to experience an initial increase for both plants from the early spring to early summer

Table 6. Light compensation point (LCP, $\mu\varepsilon m^{-2} s^{-1}$), transpiration rates (TSP, mg H_2O $dm^{-2}h^{-1}$), dark respiration (DR, mg CO_2 $dm^{-2}h^{-1}$) as they relate to a seasonal pattern in the photosynthetic capacity of 4N and 2N *Arctostaphylos*.

Phenology	Source	LCP		TSP		DR	
		4N	2N	4N	2N	4N	2N
Spring							
Preflowering	GH	10	50	0.45	0.2	-0.8	-1.0
Post flowering	GHR	20	-	5.00	-	-1.5	-
Post flowering	F	-	15	-	0.1	-	-0.6
Summer	GHR	55	80	0.65	0.2	-0.6	-1.3
Late summer	GH	10	10	5.00	2.5	-1.0	-1.0

The sample size is n = 1 in all cases.

Key:

F: field material (Kananaskis)

GH: greenhouse grown

GHR: greenhouse roof grown

Notes:

GHR and F plants are phenologically comparable. The data were derived from Fig. 8-10.

(Table 5). In the field, these values, because of the shaded environment in which the diploids occur, may not be realistic. They do represent a possible field capability that the diploid has in assimilating CO_2 at temperatures experienced under lab conditions. The temperature for optimal photosynthesis from early to late summer seems then to decrease to a seasonal low by autumn. The range of decrease for the tetraploid is from 6.5°C (preflowering to a summer condition). While the diploid range of decrease is slightly less (5°C) from the early spring values compared with the tetraploid. This may be a factor in maintaining NA at a relatively high but constant temperature which would prevent overt damage occurring under spring chinook weather conditions, and also be suited to a moderate and buffered environment in which the diploid grows.

Early Summer but One Month Later (Post flowering and Summer)

The material examined here is GHR grown. The tetraploid maintains a higher NA (Tables 3 and 4, Fig. 9), but also a concomitant higher transpiration rate. At this time the respiration of the diploid is greater than that of the tetraploid by 50%, reducing effective CO_2 fixation. Transpiration in the diploid is still very low and there is a possibility that what is observed here is due to a wounding response. The Km's and Vmax's are approximately equal. The diploid matches the tetraploid in assimilation and at conditions of lower light intensity. The temperature maxima for both are decreasing and the shift is in accord with diurnal temperature patterns so that photosynthesis may be optimal before and after noon stomatal closure. Transpiration seems to be decreasing for the tetraploid as the season progresses and is interpreted as an ever increasingly efficient use of water.

Late Summer

As described earlier, late summer appears to be the most productive part of the season in which the diploid has a 60% less NA than that of the tetraploid (Fig. 9). These twigs were not hydrated overnight and this may cast some suspicion on the pretreatments which used overnight hydration before the twigs were used in the experiment. It is possible that the reduced levels of NA observed previously were an experimental artifact and the low NA observed was due to a buildup of

ABA which might have resulted in a partial stomatal closure which can effectively reduce overall NA. ABA itself could be differentially produced in diploid and tetraploid tissue.

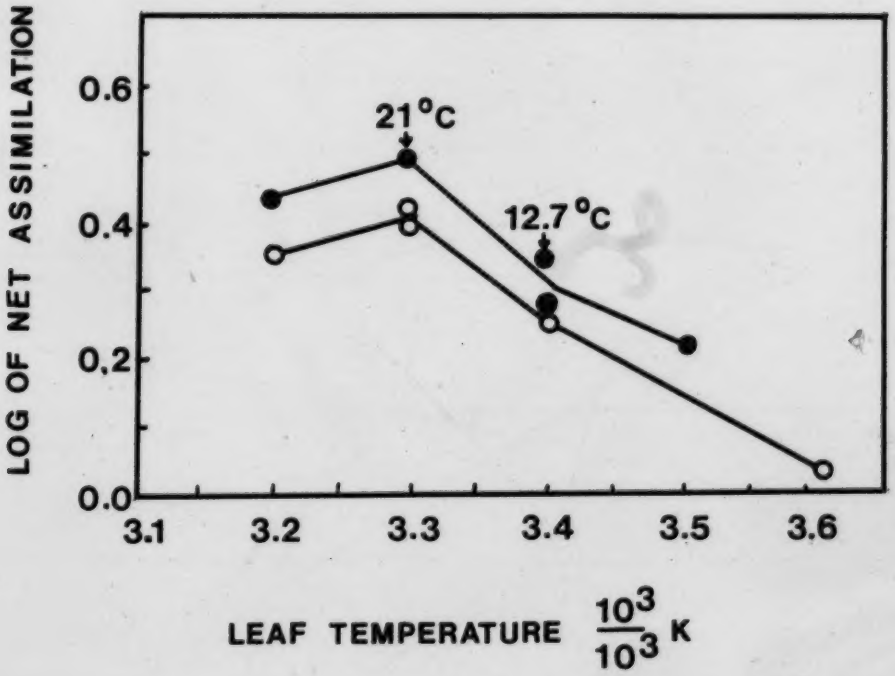
The seasonal down shift of light compensation would indicate a photoadjustment to daylength and designates bearberry as a photosynthetically early-season plant. In spring, sun angle is lower, in midsummer when rays are more direct, the tetraploid system appears efficient and maximizes the increased light intensity by shifting LCP downwards to extend the photoperiod. The diploid appears to restrict itself to higher light intensities and it is beginning to increase dark respiration as it begins to prepare for the winter. This lowering of the compensation point effectively extends the tetraploid photosynthetic period (10, 55 uE/m²/s) even in midsummer, while the diploid (50, 80 uE/m²/s) in fact shortens its photosynthetic period. Again, this may correlate with the high in chlorophyll b content in the tetraploid and the possibility of more reaction centres (to be discussed later) which are present in the tetraploid during the summer.

Temperature Response Curves

A table of seasonal optimal temperatures for NA is given (Table 5) and a graphic representation of temperature response for the two ploidies is in Fig. 12. In Table 5, comparisons between 7 and 12 April are phenologically, but not source-paired since the April 12 tissue is GHR and the other is F material. In the remaining part of April and then May, the temperature optima shift from a vernal period toward a full summer physiology (August values). For both the tetraploid and diploid they *decrease* from spring to summer. Fig 12. shows that the diploid photosynthesizes over a slightly broader temperature range (12-25°C) in which photosynthesis is at or near maximum. It has a lower optimum, 20% less, than the tetraploid which seems to have a narrower fixing temperature range (15-25°C) and an elevated temperature optimum of 22°C.

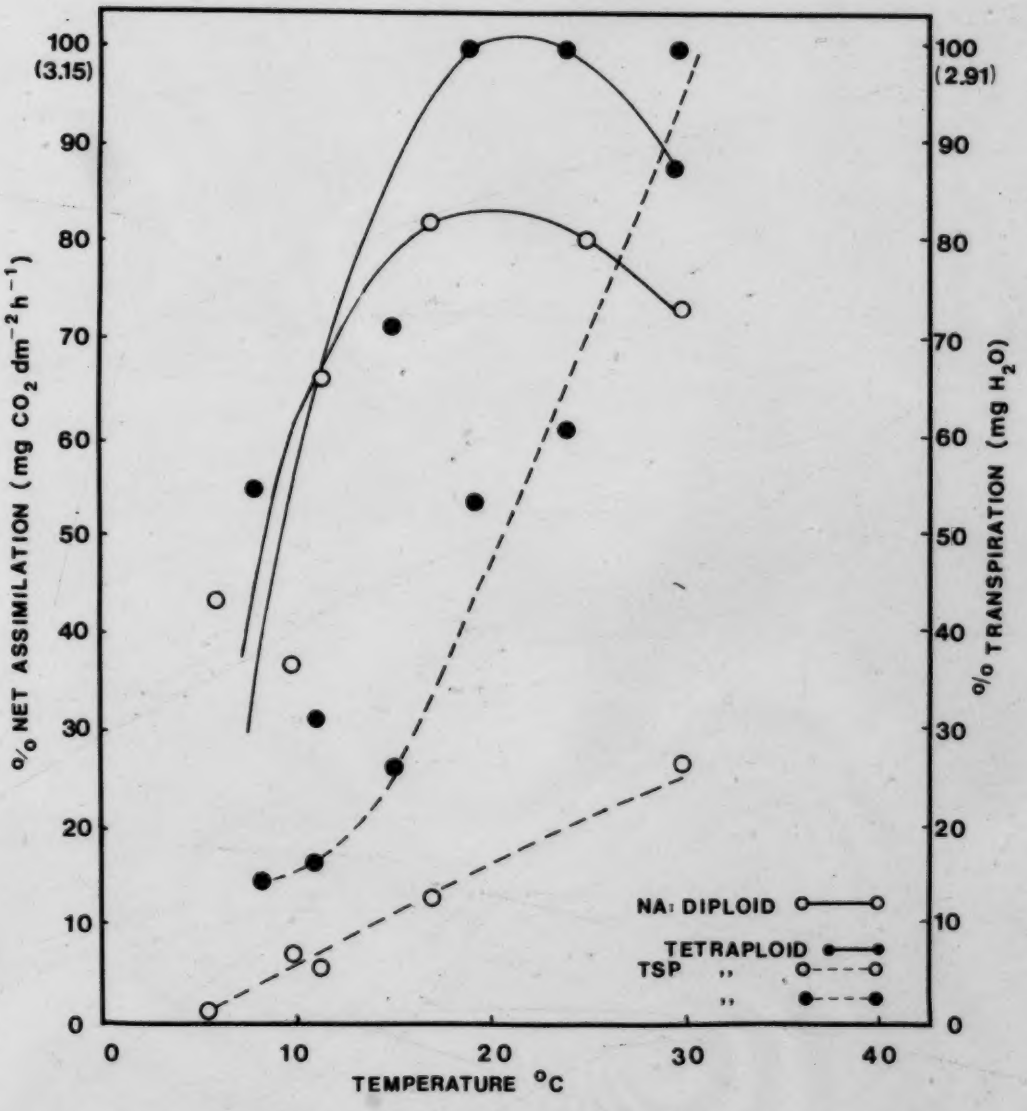
Under higher light intensities, the tetraploid experiences higher daytime temperatures and hence, operates photosynthetically in a warmer regime. Under a shaded canopy, diploid photosynthesis occurs over a broader range - optimizing the cooler temperature conditions.

Fig. 11. Log of Net Assimilation vs. Leaf Temperature.



The Arrhenius plots of net assimilation rates versus leaf temperature for diploid and tetraploid Arctostaphylos. The sample size is n = 1, and the sampling date was August 14, 1981. Rates of net assimilation are sensitive for both ploidy levels at 21°C and at 12.7°C. The diploid is graphed as o—o, the tetraploid as ●—●.

Figure 12. Temperature response curves for GHR early summer* diploid and tetraploid twigs. *April 14, 1981 light intensity was maintained at 800 $\mu\varepsilon m^{-2}s^{-1}$ the temperature maximum for the tetraploid appears at 21°C, for the diploid at 19°C.


100
(3.15)
90
80
70
60
50
40
30
20
10
0
% NET ASSIMILATION (mg CO_2 dm^{-2} h^{-1})
100
(2.91)
% TRANSPIRATION (mg H_2O)
0
10
20
30
40
TEMPERATURE °C
NA: DIPLOID
TETRAPLOID
TSP ,,
,,

In the early part of spring, the plants are emerging from a vegetatively vernal period. It would be reasonable to expect that the plants would avoid injury and possible desiccation, etc. – and utilize only the warmest days in early spring and hence, have a higher temperature optimum at the outset of the season.

The increment drop (°C) of the temperature optimum from spring to summer seems greater in the tetraploid than for the diploid, *i.e.* 6.5° *vs (Table 5)* 5°C. The diploid appears to change slowly and steadily, the tetraploid complement of chromosomes does not appear in any way to buffer the seasonal change in temperature optima drop but rather increases it.

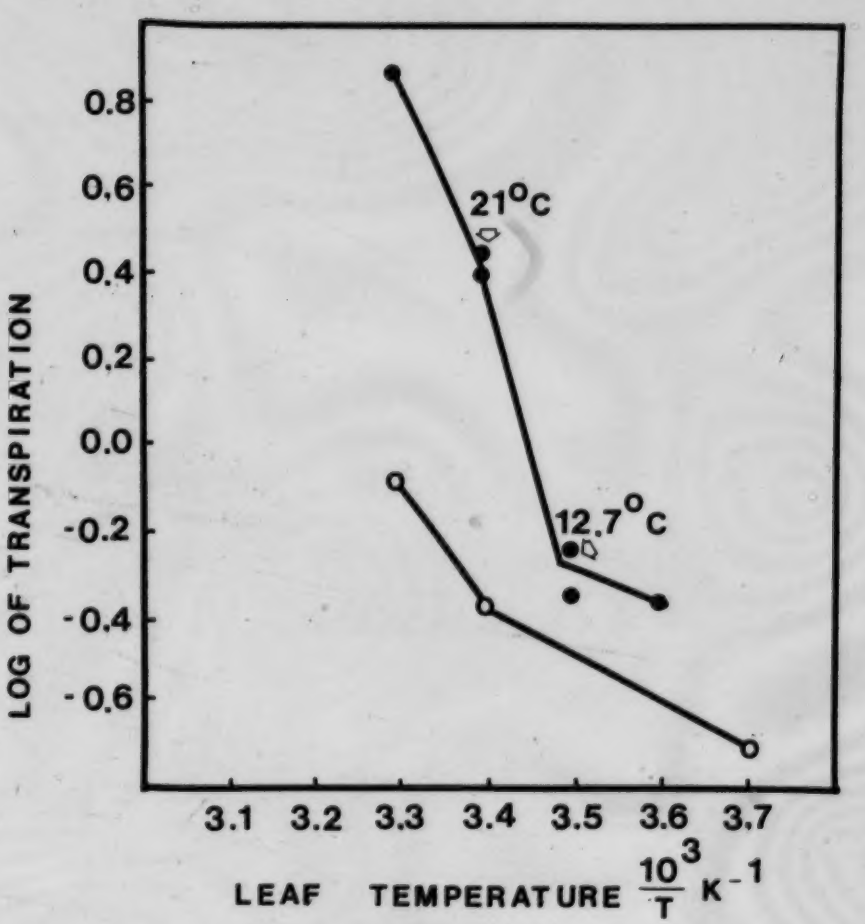
This decrease in temperature optima from spring to summer may be linked to increased photosynthetic efficiency and this in turn due to the elevated chlorophyll b levels (to be discussed) and a tighter control of water budget perhaps, affecting photophosphorylation levels ; hydrolysis in photosynthesis and the flow of electrons (see chlorophyll assay results). By a downwards shift of the temperature optima, they are avoiding transpiration losses at too high a temperature during hot summer days. Temperature optima and ranges correlate well with the subjective assessment of bearberry's preference for exposed or shaded habitats.

Arrhenius plots for August 14, summer tissue (GH) revealed two critical temperatures or sensitive areas for both NA and TSP curves in the tetraploid (Fig. 13). The rate of the reaction accelerated logarithmically at 12.7°C (as the slope increases sharply) and at 21°C resulted in decreasing rates of NA and TSP. Only the tetraploid showed these two points of sensitivity, the diploid only one (21°C) (Fig. 11).

It seems that 21°C is the maximum temperature for photosynthesis and that a doubled chromosome complement does not change the point at which an increase in temperature results in a decrease of NA. Treatment of the data by the Arrhenius transformation obscures the trend visible in Fig. 12, *i.e.* that the tetraploid has a slightly higher *optimum* temperature for NA (22°) and the diploid a slightly lower one (18.5°) C.

Above 21°C (Fig. 13), transpiration decreases for the tetraploid as NA decreases. Above 21°C, transpiration for the diploid increases as NA decreases, *viz.* the slope (m) of the diploid is less than that of the tetraploid beginning at 21°C.

Fig. 13. Log Transpiration vs. Leaf Temperature.



The Arrhenius plots of transpiration rates versus leaf temperature for diploid (o—o) and tetraploid (●—●) Arctostaphylos. The sample size is n=1, the sampling date was April 14, 1981. Rates of transpiration are sensitive at 21° and 12.7°C.

This suggests again:

1. the responsiveness of the tetraploid to water stress, a higher rate of transpiration would lead to more rapid loss of turgor of the tetraploid and an earlier stomatal closure to conserve water than in the diploid.

2. the tetraploid is more temperature sensitive. It photosynthesizes at high light/high temperature, *but* not at the expense of not maintaining a water equilibrium, while the diploid is able to continue a lowered photosynthetic rate, despite elevated temperature, in its 'low' light environment.

3. the tetraploid is opportunistic and probably carries on photosynthesis during the day in bursts if temperature rises to extremes.

Interestingly absent, or very minor, is the change of activation energy requirement in the diploid at 12.7°C in the transpiration curve. It appears or is more pronounced for the tetraploid and may be the result of the extra genome.

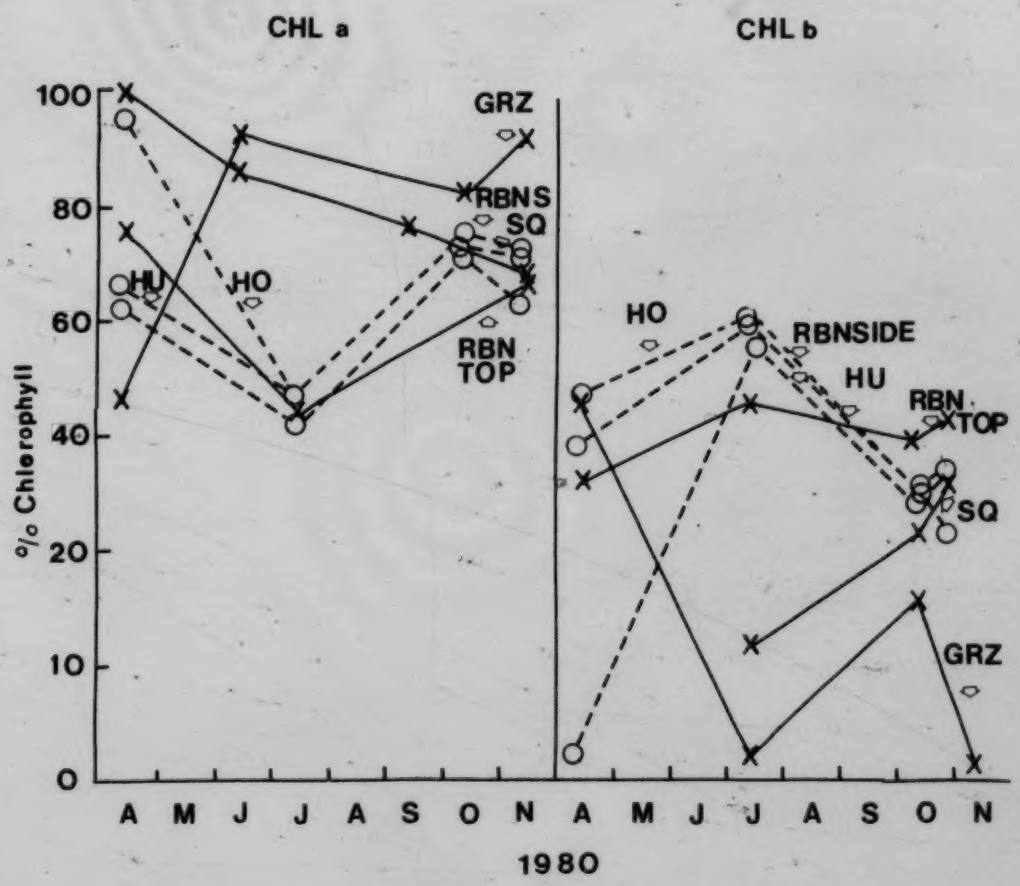
D. Seasonal Variation of chlorophyll a and b in Leaf Tissues (Fig. 14), Table 7)

After observing differences in NA capacity, experiments were focused on the subcellular level of photosynthesis, on chlorophylls a and b. Fig. 14 presents the percentage of chlorophyll per gram dry weight of leaf tissue during the growing season from April to November. Concentrations of chlorophyll from subnivean specimens are indicated by the April values.

The diploids show less of an overall change compared with the tetraploid populations over the growth season. The erratic pattern observed for GRZ may be related to storage difficulties encountered for the material while awaiting rail shipments of DMSO. In any case, it indicates the more fragile nature of *in vivo* chlorophyll preservation in leaf tissue for the diploid compared with the tetraploid, since the specimens were stressed for the same length of time.

April values represent chlorophyll contents from leaves in a winter state. For the six populations, chlorophyll a is the stable photosynthetic unit. The trend in the concentrations is for chlorophyll a to decrease in midsummer (July) and for b to increase, since a is likely to be a precursor to b (Thornber, 1975), but the change is more marked for the tetraploid. The b component could be seen to be enhancing photosynthesis in the

Fig. 14 Seasonal Variation of Chlorophyll a and b as a percentage of the total chorophyll content in young ARCTOSTAPHYLOS leaves.



Percentange is based on mg Chl g^{-1} dry weight of leaf tissue = 100 % total chlorophyll content of a leaf.

DIPLOID ✕——✕

TETRAPLOID ○- - -○

n = 7

SE were less than 0.5 and were not graphed.

tetraploids in the summer, since chlorophyll b is implicated in various roles (Thornber, 1975) The decrease is followed by a return to normal level in the fall as chlorophyll b is degraded. Within the chloroplast, chlorophyll b is thought to aid in grana formation (40–60% of the total chlorophyll is compartmentalized here in PS II) raising the density of the light harvesting pigments. This may account for increased tetraploid photosynthetic capability in late summer – even though Km remains high and bearberry affinity for CO_2, by Km definition, is lower.

Chlorophyll b plays a role in the management of cyclic and noncyclic phosphorylation. Respiration in mutant plants is low where the concentration of b is higher – and evidence indicates that dark respiration at least decreases throughout the growth season (Table 7).

Chlorophyll a may be a precursor to b. The conversion from one to another is thought to be photochemical rather than biochemical. This correlates with the increased chlorophyll b levels of the tetraploid and its highly irradiated environment. The extra light intensity is utilized here. Additionally, chlorophyll b is known to absorb wavelengths >663 nm and to transfer the energy to other reaction centres, *e.g.* P_{700}. The tetraploid extends its range of photosynthesis, increasing its photosynthetic capability again despite a higher Km.

A preliminary investigation indicates that rhizospheric nitrogen fixation occurs with maximum or optimal activity in the summer months in the bearberry community. This is contrary to the morphological evidence of Tiffney et al, 1978 who said that *Arctostaphlos* had no nitrogen fixing nodules and no nitrogen fixing ability. Chlorophyll b is also implicated again as a possible storage molecule for extra nitrogen in protein form (Thornber, 1975).

Seasonal Chlorophyll a/b Ratio in Young *Arctostaphylos uva-ursi* Leaves (Table 7)

Traditionally, the chlorophyll levels are tabulated as a ratio of chlorophyll a to b. It can be seen from Table 5 that the a/b ratio changes from >1 to <1 as the concentrations of chlorophyll b increase substantially in the tetraploids in July. The very high chlorophylla/b ratios (600, 26, 24, etc.) are the products of storage problems, these result from the degradation of chlorophyll a and b due to waterlogging of the tissue and

TABLE 7. SEASONAL CHL a/b RATIO IN YOUNG LEAVES OF DIPLOID AND TETRAPLOID *ARCTOSTAPHYLOS*

	1980	APR	JULY	OCT	NOV
DIPLOID:	Grizzly Creek	1.2	26.0	4.0	25.0
	Squirrel	600	6.0	3.3	2.0
	Ribbon Creek Top	2.0	0.8	1.4	2.0
TETRAPLOID:	Ribbon Creek Side	24.0	0.8	3.0	2.5
	Hill Open	1.6	0.7	2.5	1.7
	Hill Under	1.8	0.7	2.7	3.3

pheophytization of the chlorophyll molecules.

The tetraploid can be considered a *sun* population, the diploid a *shade* form and, in comparing the two populations in this way, there are several 'rules of thumb' with respect to other species which are contrary to results obtained with bearberry:

1. *Shade* species are known to have lower chlorophyll a/b ratios than *sun* species (Egle, 1960, Singh and Singh, 1977), *i.e.* chlorophyll a/b ratio increases as light intensity increases. Similarly, Tieszen (1970) noted that chlorophyll levels increased with increasing latitude, *i.e.* decreasing solar intensity. In *Arctostaphylos uva-ursi*, the *sun* form (tetraploid) was found to have a higher chlorophyll a/b ratio.
2. Chlorophyll b levels in general increase in *shade* plants. In *Arctostaphylos uva-ursi*, chlorophyll b increases in the tetraploid populations in the exposed, brightly insolated environment.
3. Chlorophyll a increases in the sun (Singh and Singh, 1977). Chlorophyll a/b ratio is affected by the percentage of the chlorophyll a/b – protein (not P_{700} – chlorophyll a – protein). The higher the chlorophyll a/b – protein, the lower the chlorophyll a/b ratio becomes (Alberte and Thornber, 1974).

However, while examining *shade* and *sun* leaves of *Ginkgo, Pinus* spp., *Quercus, Acer* and *Glycine*, Randall *et al.* (1976) found that low photosynthetic rates are due to the greater size of photosynthetic units (PSU), *i.e.* fewer PSU per leaf result in lower NA for the *shade* species, where PSU was defined as total chlorophyll/P_{700}. This results in large woody species being saturated at low light intensities and size differences may account for the lower photosynthetic capability of the diploid.

When considering the levels of chlorophylls a/b or b above, the ratio is depressed and eventually becomes <1. This value has not ever been reported. It is a new ratio.

In October and November the values are >1, indicating a degradation of chlorophyll b, and probably a decrease in photosynthesis.

Niches can be described as they relate to chlorophyll a/b ratios. Rabinowitch (1945) puts bearberry into perspective with other species (Table 8). In surveying the values, bearberry is midway between a fully exposed habitat – blue shade – green shade environment for midsummer values. It becomes evident here that the sampling time becomes very important since there are qualitative as well as quantitative changes in the

Table 8. Influence of the Light Field on Pigments in Green Plants

Plant type or Habit:	a:b
Alpine	5.5
Emersed H_2O	4.4
Sun exposed, land	4.36
In blue shade, diffuse sky	3.01
In green shade	2.60
Submersed H_2O	2.27
Green algae	1.39

Table 1.5 VIIII ex Photosynthesis and related processes I, Rabinowitch, 1945.

chlorophyll contents.

The role of evergreeness in plant species is overlooked. Few studies document seasonal changes, let alone relate chlorophyll content. Singh and Singh (1977) compared evergreen and deciduous leaves of several dry tropical species on a g/dry weight basis. They concluded that deciduous trees contain more chlorophyll per m^2 and per g dry weight than evergreens and presumed that this was due to the evergreen leaves existing for more than two years. The comparison here has more stimulating results. The seasonal variation which does occur here is qualitative. Further, it enhances the NA capacity of the 4N.

IV. DISCUSSION

Table 9 synoptically describes the significant physiological differences between tetraploid and diploid populations as they were observed during the summer 1979–80 and the spring of 1981. The data are an amalgam of lab and field results. Since the transpiration rates determined by a variety of methodologies from both the field and lab were virtually the same, it was supposed that other parameters could similarly be comparable, allowing a phenological scheme to be reliably derived. Most importantly it indicated that the differences shown during the experiments were due to the genetic constitution of the *Arctostaphylos* population and not to an ability of the plants to adapt to an immediate prior history *i.e.* greenhouse conditions.

In Table 9, the trends and % changes relative to springtime values are indicted for NA parameters: chl b, Km, photosynthetic temperature optimum, Vmax, DR, LCP, minimum RL and water regulation: TSP, XPP and . Midsummer was the period during which the difference appeared to be maximal. In the tetraploid the chlorophyll b levels were at their seasonal highest, Km, the lowest, Dr and TSP were decreasing and , the bulk modulus of elasticity was the largest. All of these factors contributed, as discussed in the results section, to an efficient H_2O regulation and an overall enhanced NA (300 % higher than the diploid) in the tetraploid. Briefly to recapitulate, and to interpret physiologically why NA was enhanced–the tetraploid had a lower minimum RL which perhaps facilitated CO_2 and H_2O gas exchange, chlorophyll b levels were highest and chl b is known as an auxillary light harvesting pigment which provides additional light trapping centers to utilize fully the saturated light environment; a maximum difference of 288% XPP for the diploid cf 260% for the tetraploid, indicated that the diploid is capable of sustaining a slightly higher water stress than the tetraploid and high summer 8.2×10^2 cf 1.6×10^0 agree with the midsummer XPP showing that the tetraploid is intolerant of a great loss of water from the tissue--that it would percieive a water stress more quickly than the diploid with its more rigid cell walls (higher values)--its water loss to a zero turgor is mo rapid and consequently stomatal closure would be very rapid in the tetraploid to conserve water; Πp and Π_0 values in the winter also indicate rigid cells in the tetraploid. What the tetraploid lacks in drought tolerance, it compensates for by being an opportunist in water absorption during sporadic rainshowers (Fig. 7). The physiological abilities of the tetraploid thus are

TABLE 9. SUMMARY OF SEASONAL CHANGES IN THE PHYSIOLOGICAL CAPABILITIES OF ARCTOSTAPHYLOS IN NET ASSIMILATION AND WATER REGULATION.

MAIN PHYSIOLOGICAL EVENT	PLOIDY		COMMENTS
A. NET ASSIMILATION	4N	2N	
COMPONENT EVENT			
1. CHL B CONCENTRATION			HIGHEST IN MID SUMMER (JULY)
2. KM	↑ *(207)	↑ (150)	A) TO MIDSUMMER
	↑ *(52)	↑ (39)	B) TO THE FALL
3. Ps TEMPERATURE OPTIMUM	↓ *(20)	↓ (26)	
4. VMAX	↑ (313)o	↑ (152)o	
5. DARK RESPIRATION	↓ *(34)	=	
6. LIGHT COMPENSATION POINT	↑ *(275)	↑ (533)	A) TO MIDSUMMER
	(82)	*(88)	B) TO THE FALL
7. MIDSUMMER R_L AT DAWN	MINIMUM	*(50)	I.E. 2N IS TWICE THE MINIMUM
B. WATER REGULATION			
1. TRANSPIRATION	↓ *(99)	↓ (100)	TO AUGUST/MAX Ps
2. XYLEM PRESSURE POTENTIAL	o	o	A) SUBNIVEAL/ WINTER
	(260)	(29)	B) JULY MAXIMUM DIFFERENCE BETWEEN A PRE-DAWN AND NOON READING.
3. BULK MODULUS OF ELASTICITY.	o	o	A) WINTER
	↑(1000)	↑(1000)	B) SUMMER OF WINTER
	4N >	2N	C) AUGUST 18, 1981

TABLE 8. THE PHYSIOLOGICAL CAPABILITIES OF ARCTOSTAPHYLOS UVA-URSI CHANGE IN MAGNITUDE AND DIRECTION AS THE PLANTS COMPLETE THEIR GROWTH SEASON. THESE ARE SUMMARIZED IN THIS TABLE OF PHYIOLOGICAL EVENTS VERSUS TIME. THE BOLDNESS OF THE ARROW INDICATES WHICH OF THE SHIFTS (2N'S OR 4N'S) IS GREATER; ITS LENGTH INDICATES THE DEGREE OF CHANGE FROM A SEASONAL LOW (SPRING VALUE); A * BESIDE THE ARROW WHICH OF THE PLOIDIES INITIALLY HAD THE HIGHER VALUE; AN OPEN CIRCLE (O) IS SHOWN IF THE VALUES WERE IDENTICAL FOR BOTH RACES AND AN = INDICATES NO CHANGE WHICH IS SIGNIFICANT THROUGHOUT THE SEASON. WHERE A TREND OCCURS THE BRACKETED VALUE IS THE % CHANGE (INCREASE OR DECREASE) ROMF A SPRING VALUE.

highly coincident with the high light intensity, edaphically impoverished, atmospherically xeric and unpredicatable environment in which the tetraploid is commonly found.

A second noteworthy summarization of Table 9 is the trends and shifts which occur change direction and magnitude again at mid-season for the two populations. While these are the same for both races they are exaggerated and amplified in the tetraploid. These are interpreted physiologically *e.g.* photosynthetic optimum temperature shifts to a lower value with less energy loss to respiration (a 34% decrease from spring values), perhaps indicating that the plants can photosynthesize earlier in the day and for longer periods maximizing the longer summer days, as respiration requirements of winter repair are decreased and cellular expansion and growth is limited; CO_2 partioning may be soley compartmentalized into carbohydrate storage for the coming season, a shift in lower light compensation point, all ot these might increase the period of CO_2 assimilation on a daily basis into the autumn. This would effectively extend the growth season into the cool fall days of variable precipitation and shortened daylength. Again these trends are exaggerated for the tetraploid populations. The capability of the tetraploid to extend its growth season is further verified by this population's ability to delay autumn dehydration. Changes in amplitude between day and night values of XPP occur and while the tetraploid shows a decrease in transpiration, the diploid shows an 88% increase. Thus the tetraploid seems to have a stronger tendency to a normal stomatal closure and functioning at night. Effectively, it has extended its season. Also its ability to maintain this stomatal order hints of a greater cold tolerance in the tetraploid.

Having elucidated somewhat the physiological processes between the chromosome races, the prostrate arrangement of leaves in the diploid *vs.* the tightly bunched and upright arrangement of the tetraploid can be interpreted and lend a interpretation to Shaver's (1978) observations in a physiological manner. (And so, morphology appears a mere reflection of the internal order). The diploid leaf arrangement might be viewed as a physiognomy which allows for maximum light capture in a semi-shaded environment-where water loss is not problematic. There are plenty of available seeps and local streams and as the low values show, the diploid can accomodate fairly large drops of Ψ before a permanent wilting point would be reached. For the tetraploid in its well drained soil, wind and light exposed habitat, the tightly

appressed leaves would perhaps act to minimize the water loss. Elevated levels of chlorophyll b would thus seem most beneficial in acting as an accessory pigment and might more than compensate for its peculiar leaf orientation. In conclusion, it would seem that the most important feature which enables bearberry of a tetraploid genotype to survive in and extend into xeric habitats is its ability to be a water conserver; that its survival strategy and its importance of maintaining a water balance overrides the ability to fix larger quantities of CO_2.

Because this study has primarily an aut-physiological flavour few community type measurements were made. However, one is still able to infer from the data gathered (and who can resist the temptation?) bearberry's role and specifically the role of the different ploidies within their respective communities. Where the tetraploid is found it tenaciously, to the exclusion of most other species, is the dominant shrub. A preliminary investigation into the rhizobial activity provided positive results indicated that its primary role is probably that of a nitrogen fixer in the environment. the tetraploid may also have a stronger allelopathic interaction with other species apart from and in addition to its ability to survive in depauperate habitats. This is also supported by the contrasting fact that the diploid bearberry is a codominant in its community and thus experiences competition with other species of shrubs, grasses and other nitrogen fixers. Thus it is that the tetraploid *Arctostaphylos* with all these virtues of enhanced NA and strict water regulation capabilities colonized past the mesic *Pinus contorta* communities, onto relatively bare tracts of land, forming small to vast population nodes.

V. SYNTHESIS

The physiological differences between the chromosome levels and their overall phytogeographic ranges allow for an interesting historical speculation to the Pleistocene. In highly disturbed morainal hills, ostensibly void of vegetation, xeric in both aerial and an edaphic environment, the tetraploid with its adaptive ability, would be the ideal colonizer. It has been hypothesized that tetraploid migrated from a refugial situation into these barren habitats (K. E. Denford, pers. comm., 1981). This would explain the present mosaic-type of geographic distribution where populations of diploid and tetraploid *Arctostaphylos* occur sympatrically.

In the Old World only the tetraploid (paleoploid) *Arctostaphlos* is found. One is led to suspect, since the diversity of *Arctostaphylos uva-ursi* is higher in North America and parental diploids are found here, that Western North America might be a 'center of origin' for the genus.

As is typical in any scientific study more areas of potential investigation are generated and are left unexamined due to the limited scope of the intial inquiry. One such area is the role that physiology can play in delimiting species. The two categories of bearberry found in the present study, shade-preferring and heliophilic 'species', would challenge the standard taxonomic classification of bearberry which, being based on the presehce and absence of glandular and aglandular hairs, results in no less than 5 taxa (and 3 species) (Packer and Denford, 1974), as well as some of which are unnamed. It would seem that a physio-taxonomy could provide a simplified and more sound classification, for surely the inward and internal processes manifest the phenotypic expression and not vice versa. With this is mind, a further comparative study of *Arctostaphylos* could be made between the extreme west coast 'species' of B. C. which are found on weathered granitic outcrops, the eastern 'species' of Ontario and Quebec which the author has observed colonizing silicaceously-based sand dunes, with the physiology of the *Arctostaphlos* of the present study which shows a definite preference for a calciferous substrate. The results in the context of a revised species concept would indeed be worthwhile.

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Appendix I - Site Descriptions

Cover estimates for individual species within a 5x5 m plot were estimated by the method of Daubenmire (1959) and are detailed in Holland and Coen (1982). This entailed a visual cover assessment for each canopy layer (tree, shrub, herb and bryoid). Cover of <1% was rated as a +. Note that the species list is likely incomplete as the survey was restricted to midsummer.

Squirrel: Diploid *Arctostaphylos uva-ursi* var. *adenotricha* covers approximately 50% of the ground area. Other species and covers are: a grass species 30%, *Linnaea borealis* 5%, *Epilobium angustifolium* 3%, *Rosa acicularis* 3%, *Zygadenus elegans* 2%, *Hedysarum sulphurescens* 5%, *Fragaria virginiana* 1%, *Aster ciloilatus*. Species with <1% cover include: *Aster ciliolatus, A. conspicuus, Salix* spp., *Pinus contorta* seedlings, *Shepherdia canadensis, Potentilla fruticosa, Galium boreale, Agoseris glauca, Scirpus* spp. (streamside), *Lilium philadelphicum, Anemone occidentalis* and *Spiraea lucida*.

Grizzly Creek: *Arctostaphylos uva-ursi* has 30% cover here. Other species and covers are: *Hedysarum sulphurescens* 50%, *Galium boreale* 10%, *Rosa acicularis* 15%, *Shepherdia canadensis* 10%, and *Bromus tectorum* 5%. Species with <1% cover include: *Fragaria virginiana, Achillea millefolium, Sedum lanceolatum, Stellaria* spp., *Gentiana procumbens, Penstemon confertus, Phleum alpinum, Phleum pratense, Aster* spp., *Linum lewisii, Aquilegia flavescens, Antennaria* spp., *Epilobium angustifolium, Senecio* sp. and *Castilleja* sp.

Hill Open: *Arctostaphylos uva-ursi* typically provides 60–75% of the ground cover. Other common species include: *Shepherdia canadensis* 5%, *Geum multifidum* 5%, *Juniperus horizontalis* 5%, *Aster ciliolatus* 5%, *Juniperus communis* 5%, *Galium boreale* 15%, *Senecio* spp. 10% and *Gaillardia aristata* 2%. Other species with <1% cover include: *Agoseris glauca, Potentilla fruticosa, Lilium philadelphicum, Zygadenus elegans, Hedysarum sulphurescens, Phleum* sp., *Astragalus* sp., *Zizia* sp., *Rosa acicularis, Allium cernuum* and *Smilacina* sp.

A similar community exists in HU, however the species covers are generally lower and *Arctostaphylos uva-ursi* covers only 20–50% of the ground.

Ribbon Creek: In addition to *Arctostaphylos uva-ursi*, the community consists of: *Hedysarum sulphurescens* 10%, *Spiraea lucida* 10%, *Zygadenus elegans* 10%, *Castilleja* sp. 10%, *Astragalus* spp. 7%, and *Galium boreale* 2%. Species with <1% cover include: *Senecio* spp., *Allium cernuum, Agoseris glauca, Commandra livida, Viola adunca, Geum multifidum, Campanula rotundifolia, Aster ciliolatus, Picea glauca* and *Populus tremuloides* seedlings, and *Amelanchier alnifolia*. Lichens include *Peltigera* spp. and mosses include *Tortula* sp.

Appendix II - Notes, Equations and Derivations

Photosynthesis: re. Table 5

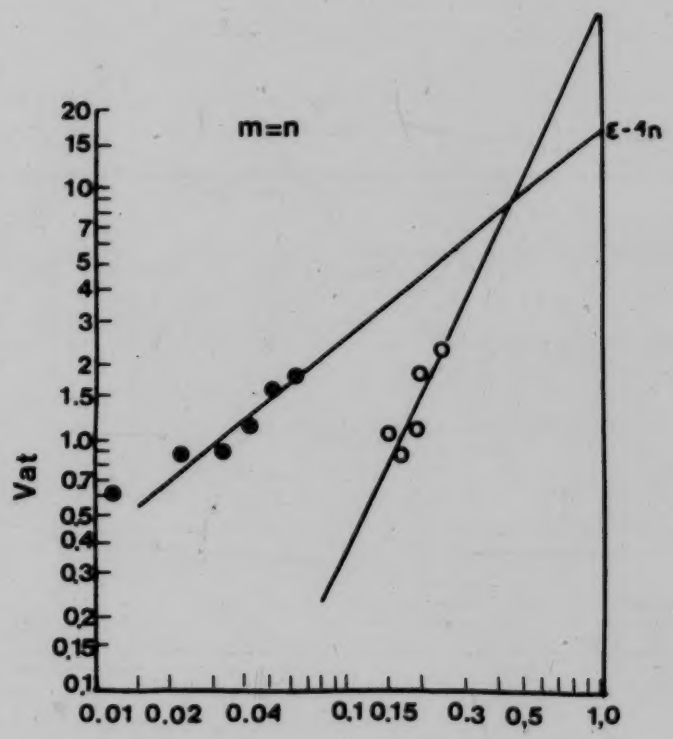
Km's and **Vmax's** were calculated by Linneweaver–Burke (LB) and Eadee–Hofstee (EH) transformations of Michaelis–Menton type NA curves. For EH transformations velocity was plotted against v/ s with the y intercept yielding Vmax and the slope m=–Km. This transformation is the most sensitive means of detecting a deviation from the Michaelis–Menton equation (Morris, 1974). The LB treatment where inverse v is plotted against v/ s gives more weight to small concentration changes, skewing the data, and raising the Km's and Vmax's to unrealistically high values. The r^2 were in bon accord and also high. EH r^2's were normally lower, and the treatment gave reasonable Km and Vmax values when compared visually with the graphs. Discretion was used against low r^2's in presenting Table 5. Either an EH or a LB transformation was used accordingly.

SI (Stomatal Index): (number of stomata per unit area number of stomata + number of epidermal cells per unit area) X 100 (Meinder and Mansfield, 1968). Usually SI is expressed in stomates/mm^2.

RL's from the field were calculated as per Turner and Parlange, 1972.

VAT ;(value average turgor): is the product of the relative volume and the turgor pressure of each cell (Tyree and Hammel, 1972).

$\mathcal{E}$ (Bulk modulus of elasticity): is a stress/strain coefficient (Scott Blair, 1969). In rheological terms it determines the amount of pressure required to deform a cell. Since the value of $\mathcal{E}$ (bars or MPa), reflects a change in the volume of tissue/unit volume–a llp change as water content changes. $\mathcal{E}$ is one of the components and along with n, and Π_0 directly limit the degree of (+) turgor in fully hydrated tissue. The large (more exponential the $\mathcal{E}$ value), the more elastic is the cell wall. $\mathcal{E}$ is analogous to the e, the coefficient of enlargement (Wilson, 1967a).
n (coefficient of linearity)(Tyree and Hammel, 1972): is derived from a log–log plot of VAT vs Relative Volume. The volume of H_2O which remains in the tissue as pressure is applied depends exponentially on n and directly on $\mathcal{E}$, the bulk modulus of elasticity. It is derived in the following manner where the slope m=n:

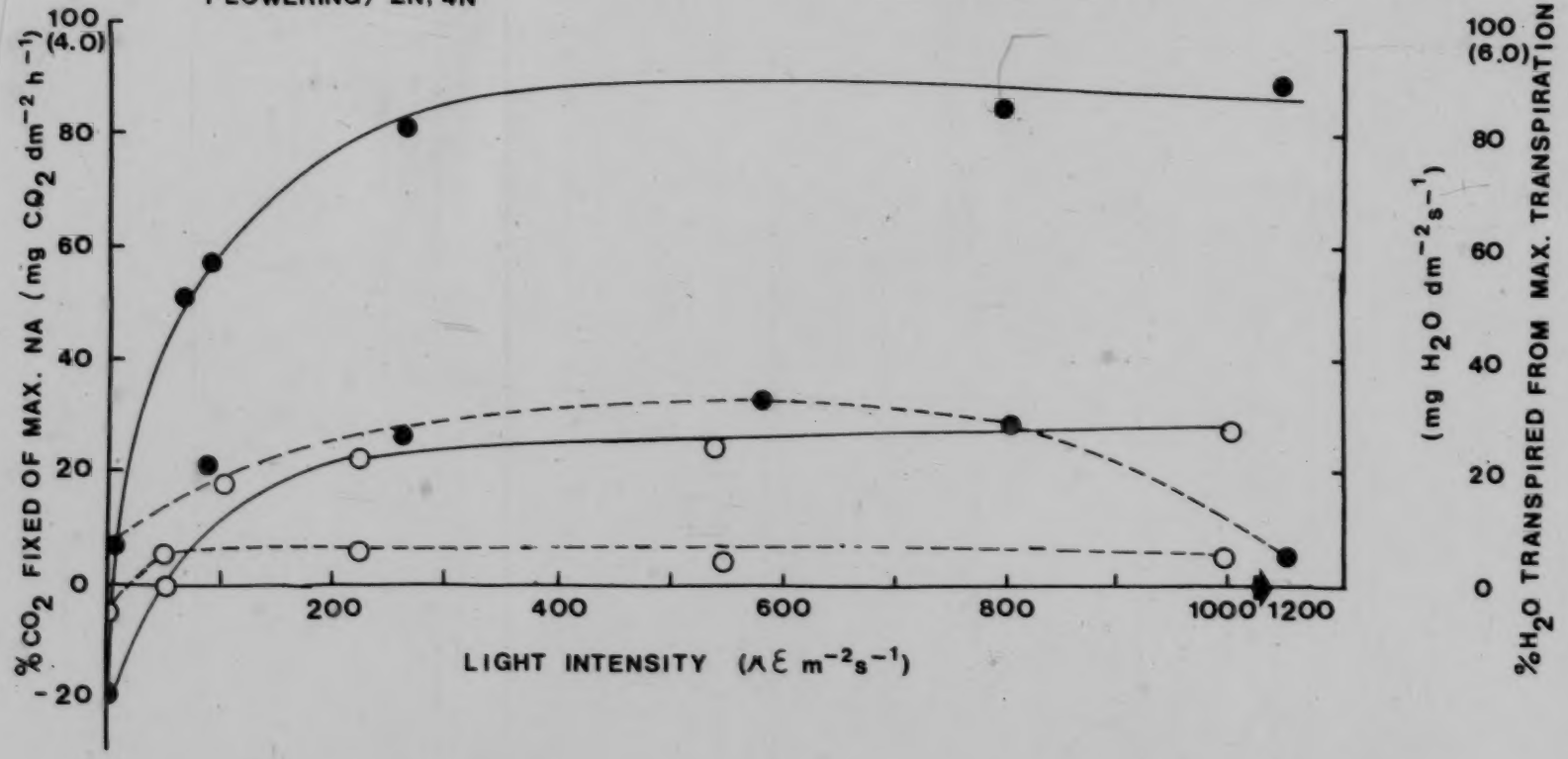


Relative volume $\frac{V-V_p}{V_p}$

Summer tissue Sq Aug 14, 2n o.

Rbnside ", 4n ●.

FIG. a SEASONAL CHANGES IN NET ASSIMILATION CAPACITY (NA) of SPRING TISSUE (PRE-FLOWERING) 2N, 4N



°C 22.5 TSP - - - O; 2N O——O Apr. 14, GHR, GRZ.

°C 17.0 TSP - - - ●; 4N ●——● Apr. 15, GHR, RBNSIDE.

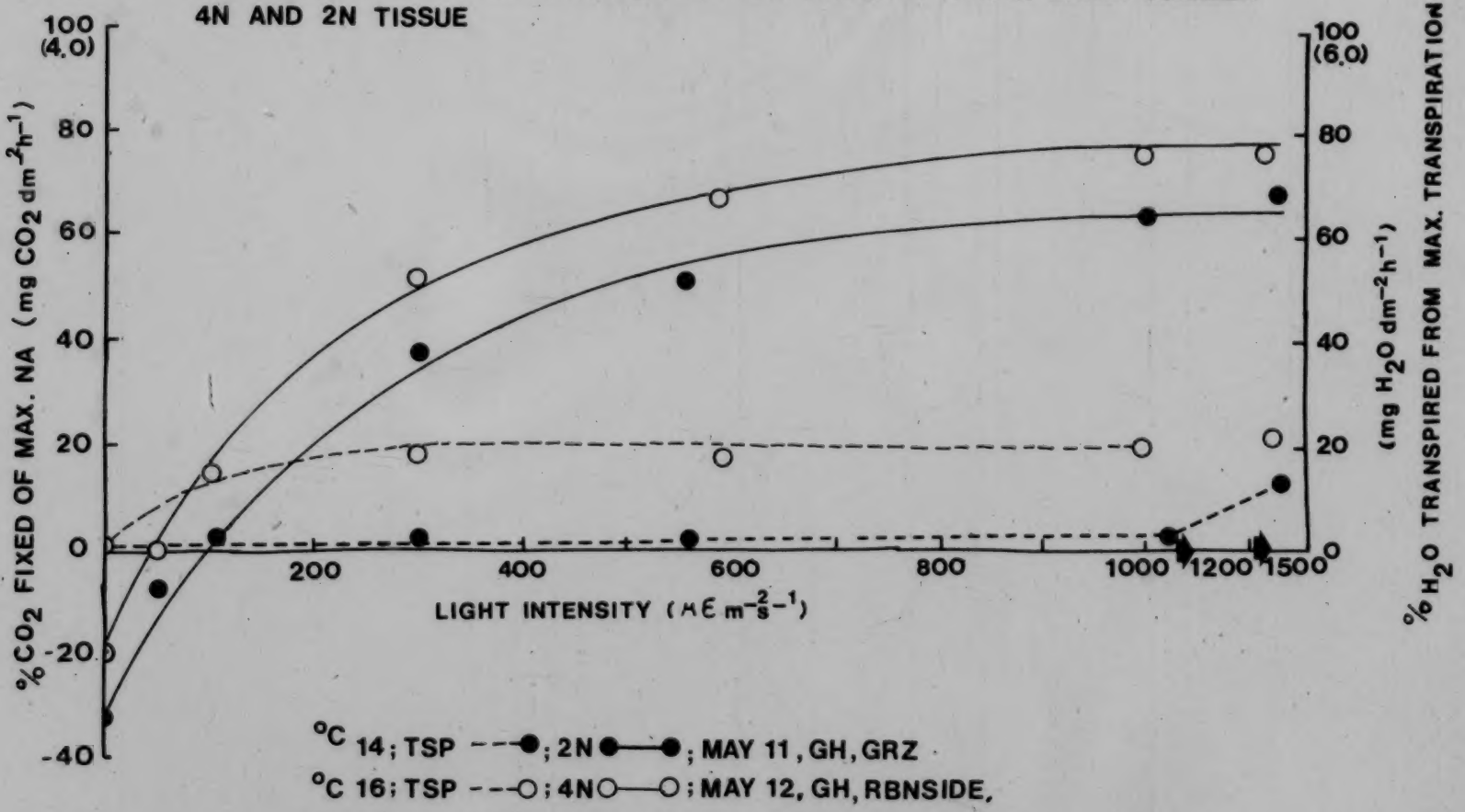



FIG. b SEASONAL CHANGES IN NET ASSIMILATION CAPACITY (NA) of EARLY SUMMER 4N AND 2N TISSUE